In situ and *ex situ* soil respiration in natural, *Acacia*-invaded and cleared riparian ecotones in the Fynbos Biome

By

Oliver Kambaj Kambol

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Supervisor: Dr. Shayne M. Jacobs

Faculty of AgriSciences

Department of Conservation Ecology and Entomology

Co- supervisor: Dr. Brian K. Mantlana

Department of Environmental Affairs,
Pretoria

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DECLARATION

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SUMMARY

Soil respiration (R_S) is a major component of CO_2 emissions and the global carbon balance. In the context of global change it of interest to understand seasonal patterns of R_S in fynbos riparian ecosystems, particularly in invaded-riparian ecotones of these Mediterranean type ecosystems (MTE's) in the Western Cape, South Africa. Riparian ecotones are three dimensional transitional zones that provide multiple ecosystem services and functions and they act as the linkage between terrestrial and aquatic ecosystems where key ecological and geomorphological processes occur. Riparian ecotones are highly prone to disturbance, and because of this reason are also vulnerable to invasion by invasive alien plants (IAPs), notably *Acacia* species.

Invasion by IAPs is considered one of the major threats to global change and biodiversity causing extensive ecological, economical, and social impacts. In south-western Cape, more than two thirds of the riparian environment is invaded to some extent, IAPs replacing the well adapted native species along river systems. In particular, impact of IAPs on soil respiration (R_S) may be relevant, with consequences for ecosystem function and services. Clearing of invaded riparian zones initiated by the Working for Water program has been a successful in eradicating alien plants within riparian areas even though recovery after alien clearing is lagging at many sites, and knowledge on repair of ecosystem function is lacking. Various studies have generated knowledge on carbon cycling and R_S in forests, savanna, grasslands, tundra and Mediterranean shrublands, but little is known about R_S in riparian zones, and even less about soil CO_2 efflux in invaded riparian fynbos riparian ecotones.

The objective of this study was to contribute to a better understanding and quantifying the effect and impact of IAPs on carbon cycling between and across riparian ecotones with different invasion status: natural, invaded, and cleared. The study areas were located in the south-western Cape and measurements of R_S, soil temperature, soil moisture, root mass, litter mass, and soil properties were carried out in riparian soils of the mountain and transitional stream longitudinal river sections, and uplands fynbos areas of six different perennial river systems. In each site, four to five transects were laid out with one sampling site of each landscape position (wet bank, dry bank, and terrestrial areas) giving a total of 12 to 15 samples per site. Soil respiration measurements were taken over a period of two years, and were done seasonally.

Results from this study showed that R_S was different among seasons with highest soil respiration rates in summer. Soil CO_2 efflux increased in response to warm and dry conditions during summer, while seasonal soil CO_2 efflux declined in autumn and winter in response to wet and cold soil conditions. The large increase in soil CO_2 efflux response to warm and dry periods when temperature was 25 to 30 °C over all riparian sites and was highest in invaded sites compared to the natural and cleared sites. A significant difference was found between sites with different statuses with invaded sites leading seasonal R_S rates. Natural and cleared sites did not differ significantly in their CO_2 efflux rates, suggesting that clearing of IAPs may put invaded ecosystems on a trajectory of restoration. There were also differences in terms of landscape positions; dry banks zones of the invaded sites had higher rates compared to wet banks and the uplands areas.

Our results further suggest that roots are the most important component of overall R_S rates, rather than microbial respiration. When we incubated soils minus roots, little difference was evident, either when viewing the results by invasion status or by landscape position, which suggest that inherent soil differences in terms of microbial respiration were not different. We also use a trenching approach to further investigate this, and though we found R_S to decline significantly, trends later suggest that decomposition of fine and course roots likely obscured the decline in overall R_S due to root respiration.

Overall, our results showed that clearing of invaded riparian zones will likely lead to successful restoration of soil functioning in terms of C cycling. Clearing of *Acacia*-invaded riparian ecotones will likely lead to a decline in root density, and which removes a major component of overall R_S. These results make the investigation of the C balance of invaded riparian ecotones and terrestrial areas critical in order to assess their contribution to regional C cycles.

SAMEVATTING

Grondrespirasie (R_S) is ‘n belangrike komponent van CO_2 uitstroming en die globale koolstofbalans. Binne die konteks van globale verandering is dit van groot belang om die seisoenale patrone van R_S in fynbos oewer ekosisteme, veral in indringer-oewer ekotone, in die Meditereense tipe ekosisteme (MTE’s) in die Wes- Kaap, Suid- Afrika te verstaan. Oewerekotone is drie-dimensioneel oorgangssones wat veelvuldige ekosisteem dienste en funksies verskaf. Hulle dien as die verbinding tussen terrestriële en water-ekosisteme waar kern ekologiese en geomorfologiese prosesse plaasvind. Oewerekotone is hoogs vatbaar vir versteuringe, en as gevolg van hierdie rede, is hul ook kwesbaar vir indringing deur indringer plante (IAPs), veral *Acacia* spesies.

Indringing deur IAPs word beskou as een van die groot bedreigings tot en met globale verandering en biodiversiteit, wat ekstensiewe ekologiese, ekonomiese, en sosiale impakte veroorsaak. In die suid- westelike Kaap word meer as twee derdes van die oeweromgewing tot ‘n mate binnegedring. IAPs vervang die goed aangepaste inheemse spesies langs riviersisteme. Die impak van IAPs, spesifiek op grondrespirasie mag substansieël wees, met gevolge vir ekosisteem funksies en dienste. Opruiming van hierdie spesifieke oewer sones, geinisieer deur die *Working for Water* program, was suksesvol in die uitroeing van indringer plante binne oewer areas. Alhoewel herstel na indringer opruiming op baie terreine agter is, is kennis oor die herstel van ekosisteemfunksies gebrekkig. Verskeie studies het kennis ontwikkel oor koolstofsiklisering en R_S in woude, savanna, graslande, tundra en Meditereense struiklande, maar daar is minimale informasie oor oewersones,en nog minder oor grond CO_2 uitstroming in indringer oewer fynbos en oewer ekotone.

Die doel van hierdie studie is om ’n bydrae te lewer koolstofsiklisering beter te verstaan, en die impak van IAPs op koolstofsiklisering te kwantifiseer tussen en oor oewerekotone met verkillende indringer statusse: natuurlik, binnegedring en skoongemaak.Die studie areas was geleë in die suid- westelike Kaap, en maatstawe van R_S, grond temperature, grondvogtigheid, wortelmassa, plantafvalmassa, en grondeienskappe is uitgevoer in oewergrond van die berg en transisionele stroom longitudinale rivier seksies, asook terrestriële fynbos areas van ses verskillende standhoudende riviersisteme. In elke area is vier tot vyf transekte uitgelê met een monsternemingsarea van elke landskapsposisie (nat bank, droeë bank en terrestriële areas)

met ‘n totaal van 12 tot 15 monsters per area. Grondrespirasie maatstawe is geneem oor ‘n periode van twee jaar, en is seisoenaal uitgevoer.

Resultate van die studie het getoon dat R_S verkil het tussen seisoene, met die hoogste grondrespirasietempo in die somer. Grond CO_2 uitstroming het toegeneem in reaksie op warm en droeë kondisies gedurende somer, terwyl seisoenale grond CO_2 uitstroming afgeneem het in herfs en winter in reaksie op nat en koue grond kondisies. Die grootste toename in grond CO_2 uitstroming was in reaksie op warm en droeë periodes wanneer temperature gewissel het tussen 25 tot 30 ˚C oor alle oewersones, en was die hoogste in binnegedringde sones, vergeleke met die natuurlike en skoongemaakte terreine. ‘n Beduidende verskil is gevind tussen terreine met verskillende statusse in CO_2 uitstromingskoerse, ‘n aanduiding dat opruiming van IAPs binnegedringde ekosisteme op 'n trajek van restorasie plaas. Daar was ook verskille in terme van landskapsposisies; droeë bank sones van die binnegedringde terreine het hoër tempos gehad, vergeleke met die nat bank en die hoogland areas.

Ons resultate dui verder aan dat wortels, eerder as mikrobiologiese respirasie, die mees belangrike komponente van R_S koerse uitmaak. Toe ons grond minus wortels inkubeer, is min verskille opgemerk, as gekyk word na die resultate deur indringer status of landskapsposisie, wat toon dit dat inherente grondveskille in terme van mikrobiologiese respirasie nie verskillend is nie. Ons het verder ook 'n sloot-benadering gebruik om verdere ondersoek hierop in te stel, en alhoewel ons bevind dat R_S aansienlik afgeneem het, dui neigings later aan dat afbraak van fyn en growwe wortels die afname in gehele R_S as gevolg van wortel respirasie waarskynlik verdoesel.

Ons resultate dui daarop dat opruiming van binngedringde oewers klaarblyklik sal lei tot suksesvolle restorasie van grondfunksionering in terme van C siklisering. Opruiming van *Acacia*- binnegedringde oewer ekotone sal vermoedelik lei tot ’n afname in worteldigtheid, en wat ‘n belangrike komponent van die gehele R_S kan verwyder. Hierdie resultate maak die ondersoek van die C balans van binngedringde oewer ekotone en terrestriële areas krities, om sodoende hulle bydrae tot streeksgewyse C siklusse te asseseer.

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CHAPTER 1

A LITERATURE REVIEW OF SOIL RESPIRATION, WITH EMPHASIS ON REPLACEMENT OF NATIVE WITH ALIEN INVASIVE RIPARIAN TREES IN THE FYNBOS BIOME

1.1 GENERAL INTRODUCTION ON SOIL RESPIRATION

Soils are the major reservoir of carbon (C) in terrestrial ecosystems, containing more than two-thirds of the total C in the terrestrial part of the biosphere (Lin et al., 1999). Soils are very important in the terrestrial C cycle due to their role in cycling and storage of C (Raich et al., 2002). Soil respiration (R_S) is the release of CO_2 from soils of terrestrial ecosystems and is one of the major pathways of C flux between the earth and the atmosphere (Schlesinger and Andrews, 2000), second only to gross primary productivity (GPP) (Davidson et al., 2002). Soil respiration represents the combined respiration of roots, mycorrhizae and soil microorganisms (Rustad et al., 2000) and is also referred to as soil CO_2 efflux (Kutsch et al., 2008; Rustad et al., 2001), is an essential component of biosphere-atmosphere interactions (Kutsch et al., 2009; Luo and Zhou, 2006). Soil respiration is an integration of several ecosystem processes (Janssens and Pilegaard, 2003; Kutsch et al., 2008) with many factors reported to influence rates of soil CO_2 efflux. These include temperature (Winkler et al., 1996; Schleser 1982), soil moisture (Howard and Howard, 1979; Davidson et al., 1998), root mass, litter input, microbial and soil nitrogen concentrations (Fang and Moncrieff, 2001; Buchmann 2000), vegetation and substrate quality (Raich and Schlesinger, 1992), net ecosystem productivity (NEP) (Raich and Potter, 1995). Nearly 10 % of the atmosphere's CO_2 flux passes through soils each year, which is more than 10 times the CO_2 released from fossil fuel combustion (Raich and Tufekcioglu, 2000; Schlesinger and Andrews, 2000).

An important determinant of R_S is the soil organic matter (SOM) pool, which is different for soils within different ecosystems. This is the proximate factor influencing R_S, which determines the potential for R_S, while soil temperature and soil moisture determines the actual rates of R_S. The two major components of R_S are autotrophic and heterotrophic R_S. The heterotrophic production of CO_2 by soils is dependent to a large degree on microbial decomposition of SOM which, like other physiological, ecological, chemical and biochemical reactions, is temperature and moisture dependent (Davidson and Janssens, 2006; Mantlana 2008). The total SOM in soils is a function of input from leaf and detritus material and output mainly as CO_2 efflux from the soil surface, though methane (CH_4) efflux and hydrological leaching of dissolved and particulate

carbon compounds are also relevant (Davidson and Janssens, 2006). Therefore, the rates of R_S vary by ecosystem (Raich and Schlesinger, 1992), and are also highly spatially variable within one location or site (Law et al., 2001). A positive co-variation between soil temperature and soil moisture is commonly observed in Mediterranean climate ecosystems where the wet season is often cooler than the hot and dry summers (Joffre et al., 2003). The second important component is autotrophic R_S, thus overall, R_S is an integration of numerous ecosystem processes (Fang and Moncrieff, 1999; Janssens and Pilegaard, 2003) including plant productivity, photosynthesis and root activity. Factors like soil pH, the activity of vegetation, litter fall, decomposition dynamics and the amount and residence time of rainfall (Zak et al., 2000; Andersson and Nilsson, 2001; Raich and Schlesinger, 1992; Davidson et al., 2000) are also of importance. Therefore, the cycling of C through soils is determined by vegetation and SOM dynamics.

Several studies have evaluated the spatial variability of R_S across the landscape and have observed important differences in soil CO_2 efflux associated with spatial location (Pacific et al., 2010). It is been noted that significant differences in R_S have been found between difference slopes within the landscape in the northern hemisphere (Pacific et al., 2009), e.g. between riparian areas and upland areas (Pacific et al., 2009; Riveros-Iregui et al., 2008; Webster et al., 2008), which may be attributed to differences in the distribution, quantity, and quality of organic matter (Epron et al., 2004). Some recent literature demonstrated that at large scales (km^2), the spatial variability of R_S is organized by landscape morphology and structure and that the large spatial variability can even result in opposing responses of R_S to climatic forcing (Riveros-Iregui and McGlynn, 2009; Pacific et al., 2009). Mantlana (2008) also showed that soils in different landscape positions around and swamp in Botswana showed different soil CO_2 efflux rates, and even different sensitivity to temperature and moisture controls. A deeper understanding of how R_S is controlled within different landscapes is thus needed.

Degradation is the loss of vegetation structure, productivity and biodiversity (Lamb and Gilmour, 2003). A degraded area will still contain some of the native species, but it will have lost its pre-disturbance ecological integrity. This may take place as a result of over exploitation and repeated disturbances (Lamb and Gilmour, 2003). This leads to an altered vegetation cover and goes hand in hand with exotic species that colonize degraded sites. This can result in erosion, landslips and changed fire regimes, water pollution and siltation of water bodies. Collectively, these can cause the degraded site to loose its productivity and many of the ecological goods and services that were formerly provided (Lamb and Gilmour, 2003; Laser et al., 2009). Any

loss of plant productivity will result in a reduction of the R_S rate. Both aboveground and belowground components of R_S are affected and collectively, and in the long term, soil carbon pools (SCPs) will be affected if vegetation is lost though disturbance. On the other hand, if denuded landscapes are, over time, replaced by alien invasive species, or other types of vegetation that may not be the original vegetation, R_S will also be affected. This is the case in the south-western Cape where fynbos riparian systems and adjacent uplands of the slopes are completely invaded by *Acacia* spp. A dense monoculture developed, suffocating the native plants and resulted in biodiversity loss. Once the non-natives were removed, land lay bare for long periods, making it vulnerable to erosion. This increased erosion potential can have negative impacts on the geomorphological processes downstream.

Invasive alien plant (IAP) species are widely recognized as a main threat to biodiversity and ecosystem stability (Gorchov and Trisel, 2003; Callaway and Aschehoug, 2000; Vitousek et al., 1987). Riparian ecosystems tend to be much more susceptible to invasions because of their location on the landscape where water, nutrients, and the impacts of disturbances accumulate. Their presence and proliferation lead to the displacement of indigenous plant species (Mack et al., 2000). Invasive plant species can alter geomorphology, hydrology, biogeochemistry, and disturbance regimes within the ecosystems they invade and they may have profound economic consequences (Macdonald et al., 1989). The dense and aggressive growth of *Acacia mearnsii* creates monoculture stands and significantly alters the system it invades by changing the availability of resources for native species (Levin et al., 2003; Meyerson et al., 2000; Levin et al., 2006). They can also alter erosion rates and stream geomorphology by stabilizing river banks resulting in down cutting of stream channels thereby limiting the river's ability to meander and flood (Graf 1978). Changes to C and N biogeochemical cycling include decreasing litter quality and increasing decomposition rates, fine sediment accumulation, increasing above and belowground pools of C and N, and increasing net ecosystem exchange (Ashton et al., 2005; Allison and Vitousek, 2004; Drenovsky and Batten, 2007). Several found that invasive species have an impact on biogeochemistry due to the introduction of N fixing species into N limited soils of Hawaii (Vitousek et al., 1987; Hughes and Denslow, 2005; Mack and D'Antonio, 2003) and Yelenik et al. (2004) in fynbos South Africa. However, IAPs also tend to increase above ground biomass and modify litter quality, which leads to an increase in net soil carbon pools (SCPs) and N mineralization within the invaded systems (Drenovsky and Batten, 2007; Evans et al., 2001; Mack et al., 2001). Changes in both the SCPs as well as above and belowground

biomass suggest that primary and secondary controls on R_S are modified in landscapes invaded by transformer species, end hence, R_S rates are affected.

Soil respiration involves several processes; including the rise in CO_2 availability directly impacts photosynthetic processes, evoking a broad range of physiological and morphological responses in plants. These vary among species, depending on differences in photosynthetic pathways, intrinsic growth rates, and other properties. Common responses include changes in growth rates (Poorter et al., 1996; Poorter et al., 1998), allocation patterns (Bazzaz 1990), water use efficiency (Eamus 1991), and nutrient uptake rates (Jackson and Reynolds, 1996). Most of southern Africa's plant species are of the C_4 type (Milton 2004), whereas the entire invasive alien species are C_3. C_4 plants use nitrogen more efficiently so can out-compete C_3 plant in undisturbed ecosystem. However, global change is likely to change this competitive balance (Dukes 2000). Vegetation clearing, agriculture practices and increases in atmospheric nitrogen all increase nitrogen availability in the soil, giving C_3 plants an advantage over C_4 plants. Furthermore, an increase in atmospheric CO_2 will improve nitrogen-use efficiency of C_3 photosynthetic path way, giving them an even greater advantage over C_4 plants (Milton 2004; Dukes 2000). Furthermore, Chapin et al. (1994) found evidence for P limitation on young soil where N fixers are dominant in ecosystems that, weathering rates might be too slow to supply enough P (Primack 2004). These repulsive impacts may lead to further changes in community structures by inducing secondary invasion of woody species resulting change in soils biochemical processes. Rates of R_S are largely CO_2 production in the soil and CO_2 transport from the soil to the atmosphere.

Soil respiration can be used as an indicator of ecosystem functioning reflecting changes in ecological processes in Mediterranean-type environments (MTE's) (Oyonarte et al., 2012). This is because R_S is a biogeochemical process involving several processes that act at different scales and which, in turn, are influenced by a wide number of biotic and abiotic factors observed at different hierarchical levels (Luo and Zhou, 2006). Part of the CO_2 production in soils is related to the metabolic activity of plant roots and associated mycorrhizae (Högberg et al., 2001; Hanson 2000; Oyonarte et al., 2012), while another important fraction is associated with the heterotrophic respiration of microbial communities (Giardina et al., 2004). The proportion of these components varies from one ecosystem to another (Raich and Schlesinger, 1992; IPART. 2011). This suggests that R_S has great potential as an indicator of ecosystem metabolism, by linking below and aboveground processes that respond to a large number of factors controlling metabolic processes (Ryan and Law, 2005). However, basal respiration have been shown to

decrease by > 30 % after clearing of IAPs. Also, clearing of a younger invaded site markedly decreased basal respiration by 54 % after removal of both *Acacia* trees and debris. Removal processes resulted in reducing soil C and N by 35 % in a Mediterranean coastal dune ecosystem (Marchante et al., 2008). In the circumstance of a method for monitoring ecosystems health in the most degraded areas of the fynbos riparian, R_S may be considered as an ecosystem attribute that reflects early changes in ecological processes and indicates that a more significant change is expected to occur. Therefore, as a vital sign, it could be an ideal indicator of the ecosystem that can be used universally and at very different scales, although its use would have to be adjusted to specific ecosystem conditions (Davis 2005; Oyonarte et al., 2012).

1.2 CARBON IN THE EARTH SYSTEM, AND ITS IMPACTS ON CLIMATE

Photosynthesis and respiration are the two opposing processes that drive the global carbon cycle. It is predominantly a gaseous cycle, with CO_2 as the main vehicle of flux between atmosphere, hydrosphere and biota. Historically, the lithosphere played only a minor role; fossil fuels lay as dormant reservoirs of C until man's intervention in recent centuries. Human activities, primarily the burning of fossil fuel and change in land cover and land use, are nowadays believed to be increasing the atmospheric concentration of greenhouse gases (GHGs). This alters energy balances and tends to warm the atmosphere which will result in climate change. Such changes in climate will have significant impact on local and regional hydrological regimes, which will in turn affect ecological, social and economical systems. Therefore, the study of the various impacts of climate change on hydrological regimes over the coming century has become a priority, for research on water and watershed management and restoration strategies.

Soils represent the largest terrestrial stock of C, holding approximately 1.500 Pg (10^{15} g) C in the top metre (Kutsch et al., 2009). This is twice the amount held in atmosphere and thrice the amount held in terrestrial vegetation. Soil respiration is the major path by which CO_2 returns to the atmosphere after being fixed via photosynthesis by land plants (Merbold et al., 2011), second only to GPP (Rambal et al., 2003; Raich and Schlesinger, 1992; Davidson et al., 2002a) and accounts for about 25 % of the global CO_2 exchange (Jia and Zhou, 2008). Dry atmosphere consists almost entirely of nitrogen (78.1 % volume mixing ratio) and oxygen (20.9 % volume mixing ratio), together with a number of trace gases such as argon (0.93 % volume mixing ratio), helium (0.75 %) and GHGs such as carbon dioxide (0.035 %), nitrous oxide (0.903%

volume) and ozone (0.35 % volume ratio) (IPCC 2007; Marcantonio et al., 1995). The actual CO_2 stock in the atmosphere is about 750 Pg of C. In addition, the atmosphere contains water vapour as well as clouds and aerosols which influence the Earth's temperature (IPCC 2007).

There are five major global carbon pools. The largest pool is called the oceanic, followed by the geologic pool comprising 4000 Pg of coal and 500 Pg each of oil and gas (Figure 1.1). The terrestrial carbon pool is the third largest pool comprising soil and the plant or vegetation components. The SCP comprises two components: the SOM pool and the soil inorganic C pool (Eswaran et al., 1995), with a total SCP of about 2300 Pg to 1 m depth. The vegetation pool is estimated at 560 Pg, making the terrestrial C pool at about 2860 Pg. The atmospheric pool is slightly higher than the vegetation pool with 760 Pg and increasing at rate of 3.2 Pg C per year. Thus, the SCP of 2300 Pg is about 4.1 times the biotic-vegetation pool and about 3 times the atmospheric pool. In comparison, the terrestrial C pool of 2860 Pg is about 57 % of the geologic pool and about 4 times the atmospheric pool. All these pools are interrelated with each other. For example, 60 Pg carbons are exchanged in each direction among biota-vegetation and the environment each year. In comparison, only 6.3 Pg per year is emitted by fossil fuel combustion and 1.6-2.0 Pg per year by land-use change. Thus enhancing photosynthetic fixation and sequestering even 5 % of the photosynthetic C into the terrestrial ecosystems can drastically offset the industrial emissions. Another challenge are to determine which of the five source is contributing to the increase of CO_2 concentration in the atmosphere, and which pools are potential sinks of atmospheric CO_2. The geologic pool is an apparent and quantifiable source. Another obvious but not easily quantifiable source is the tropical deforestation and the attendant biomass burning. So far emission of CO_2 and other greenhouse gases (GHGs) by soil and ecosystem degradation is an important but neither an obvious nor an easily quantifiable source. Each year, world soils release about 4 % of their pool (60 Pg) into the atmosphere, which is 10 times the anthropogenic combustion. The exact magnitude of the loss is known, and may in fact be much greater because of human perturbations, and soil and ecosystem degradation. On the other hand, the so-called missing carbon may also be absorbed by soils and other ecosystems. However, annual R_S rate is low in boreal forests, intermediate in temperate forests and high in tropical forests (Luo and Zhou, 2006).

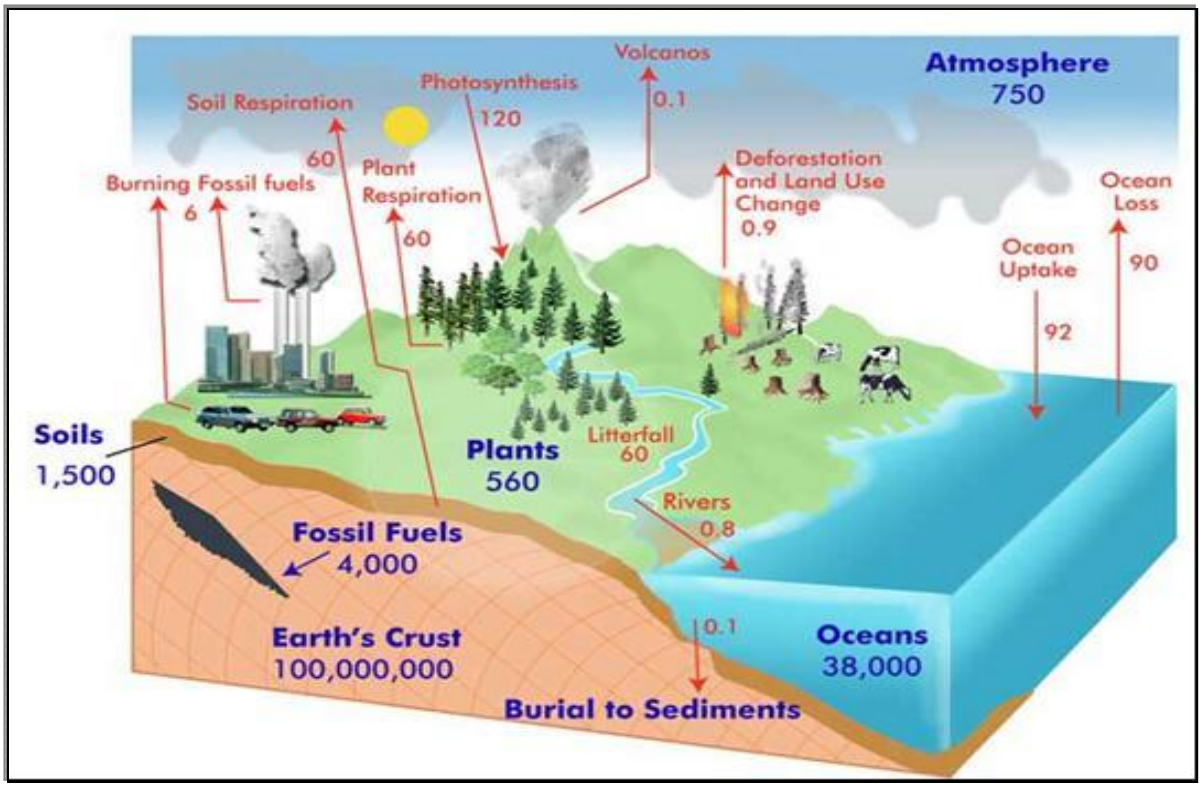

Figure 1.1: A simplified diagram of the global C cycle. Above and below-ground C stocks and fluxes affected by environmental change from globe C projects. Pool sizes, shown in blue, are given in petagrams (Pg) of C. Red arrows represent the fluxes in Pg per year Source: www.globe.gov/projects/carbon.

The atmosphere contains approximately 750 Pg C y^{-1}, most of which is in the form of CO_2, with much slighter amounts of CH_4 and various other compounds (IPCC 2001; Raich and Potter, 1995). Although this is considerably, less C than that contained in the oceans or shell, C in the atmosphere is of vital importance because of its influence on the greenhouse effect and climate. Being a major contributor to the atmospheric CO_2, R_S is a major component of C budget (Tufekcioglu et al., 2001). As stated earlier, the CO_2 efflux released through R_S is a GHG that will continue to trap energy and increase the global mean temperature if concentrations continue to rise. There has been a rapid increase in atmospheric concentration of CO_2 and other GHGs into the atmosphere. Therefore, as global temperature (GT) rises, the rate of R_S across the world will increase thereby leading to a higher concentration of CO_2 in the atmosphere, again leading to higher GTs. For example, a 20 % increase in R_S has been estimated to contribute 2 to 3 times more CO_2 to the atmosphere than the amounts released per year by

combined fuel and land use changes (Lal et al., 2003). Thus, the terrestrial and ocean ecosystems act as buffers to maintain the global temperature in a habitable range.

Land clearing and combustion of fossil fuel are two major causes for elevating atmospheric CO_2 concentrations from 280 to more than 360 ppm in the last 200 years (Keeling et al., 1995). Studies have shown that, this increase in atmospheric CO_2 is a result of human activities that has occurred over the last 150 years including the burning of fossil fuels and deforestation because it is a GHG. This increase is believed to be causing a rise in GT (IPCC 2007; Luo and Zhou, 2006). Other study has predicted that the total amount of C released annually to the atmosphere increases with the global deforestation rate (Yamagata and Alexandrov, 1999). Twenty percent of existing forests and woodlands have been logged and/or converted to other uses worldwide since the pre-industrial era (Richard 1991). Earth system plays a double crucial role on soil C cycling and may be acting as source and sink at the same time due to C accumulated and C emitted. The C cycle is a balance system when all sources are equal to all sinks, therefore the C cycle can be said to be in equilibrium and there is no change in the size of the pool over time.

1.3 CARBON TURNOVER IN THE SOILS AND CONTROLS ON CARBON DIOXIDE EMISSIONS

Globally, forests store vast pools of C and even small shifts in the balance between photosynthesis and ecosystem respiration can result in a large change in the uptake or emission of CO_2 from forests to the atmosphere. Tropical, temperate, and boreal forests cover about 4.1 billion hectares of the earth's land surface, with forest ecosystems containing up to 80 % of all aboveground terrestrial C and about 40 % of all belowground terrestrial C (Dixon 1994). Rates of both plant production and decomposition are related to latitudinal climatic gradients spanning the poles to the equator (Reich and Bolstad, 2001). However, the net C accumulation by an ecosystem over the decadal time frame depends more heavily on time since disturbance than on climate (Chapin et al., 1996). Large quantities of C stored in forest ecosystems for decades to centuries can be released to the atmosphere over short time steps following disturbance (Gu et al., 2004; Page et al., 2002; Schulze et al., 1999). Therefore, net C accumulation by forest ecosystems depends fundamentally on forest age and natural disturbance regimes, and land use practices play a key role in regulating C cycling and storage (Houghton 2001). Rising atmospheric CO_2 concentration due to land use change and fossil fuel combustion has resulted in an increase in the global mean surface temperature by 0.76 °C in

the past 150 years and is predicted to increase by 1.5 to 6.4 °C in the next 100 years (IPCC 2007; Houghton 2000).

Temperature substantially impacts almost all aspects of terrestrial C (Canadell et al., 2007; Luo et al., 2007; Luo and Zhou, 2006) and elevated global surface temperatures are likely to enhance C fluxes potentially feeding back to a build-up of atmospheric CO_2 concentration and climate dynamics (Rustad et al., 2001; Luo et al., 2001; Luo et al., 2007). Climate warming influence on ecosystem and global C cycling is primarily through two major C fluxes, namely autotrophic respiration and heterotrophic respiration (Wan et al., 2005). The balance of these two determines whether ecosystems will act as C sources or sinks with climate change (Wan et al., 2005). Since temperature affects almost all chemical and biological processes (Wan et al., 2005), climate warming may directly influence C processes in terrestrial ecosystems through changes in plant photosynthesis is growth and R_S (Shaver 2000). The rates of soil CO_2 efflux vary by ecosystem (Raich and Schlesinger, 1992) and are the major component of whole ecosystem respiration, which in turn explains much of the continental gradient of the net C balance (Valentini et al., 2000). In Europe, most of croplands are assumed to lose organic C (Janssen et al., 2005). The loss may be enhanced by climate warming (Cox et al., 2000; Kirschbaum 1995) and the emitted CO_2 may in turn reinforce climate warming. However, current models of the global C cycle seldom explicitly include these processes.

Soil respiration increases when ecosystems are exposed to elevated levels of CO_2 (Moutinho-Pereira et al., 2004). Numerous free air CO_2 enrichment (FACE) studies have been conducted to test R_S under predicted elevated CO_2 conditions. Soil respiration has been found to increase up to 40.6 % in a sweet gum forest in Tennessee and poplar forests in Wisconsin under elevated CO_2 conditions. A significant amount of C comes from the gradual decomposition of dead plant matter and the oxidation of soils, especially peat. This is more than the entire transport sector emissions produced by either the United States of America or China (Alpert et al., 2006). Deforestation in tropical countries is in itself a major cause of GHGs emission. When trees are burned, they release C which goes straight up in smoke. Melting of the world ice sheet is another possible effect of CO_2 warming (Harper et al., 2005). Changes in the amounts and timing of rainfall events will likely affect ecosystem processes, including those that control C cycling and storage. Soil CO_2 flux is an important component of C cycling in terrestrial ecosystems, and is strongly influenced by climate (Houghton 2000). As CO_2 levels rise some of the effects include: GT increases, accelerated melting of glaciers and permafrost in arctic and Antarctic regions, rise in sea levels and changes in weather patterns (Harper et al., 2005;

Hansen et al., 1981). Further intensification of the hydrological cycle is expected to increase not only the frequency of wet spells and severe droughts but also change the land area of dry and wet ecosystems (IPCC 2001; Hansen et al., 1981). It is, however, unclear how fluxes and storage of C in terrestrial ecosystems will respond to extreme changes in precipitation (Borken et al., 2006).

Soil moisture may limit or inhibit microbial decay of soil organic matter (SOM) at high and low water contents, whereas root and microbial respiration within the rhizosphere may be less affected by low soil water contents, because many plants might compensate for soil water deficit in surface soils by water uptake from wetter, deeper soil depths (Borken et al., 2006). For example, rainfall events in grassland soils generate short-term pulses of soil CO_2 following prolonged dry periods (Fay et al., 2003; Xu and Baldocchi, 2004). This may have the greatest impact on arid ecosystems, and also some MTE's. It has been shown that R_S in MTE's exhibits dynamic changes within a rainfall cycle (Gasith and Resh, 1999). Some studies have shown that rainfall induced-pulses of R_S can account for 5-10 % of net ecosystem productivity in mid-latitude forests (Lee et al., 2004) and up to 90 % of the late-season ecosystem respiration in semi-arid grasslands (Xu and Baldocchi, 2004). Ultimately, rainfall-induced fluxes may determine whether ecosystems function as sources or sinks of atmospheric CO_2 (Shim et al., 2009). The coupling of autotrophic and heterotrophic respiration may help elucidate the dynamic responses of R_S to rainfall variability (van der Putten et al., 2009).

Soil is the largest terrestrial C pool (Post et al., 1982). Stored soil C result from imbalance between organic matter (OM) produced by plants and its decomposition back into the atmosphere as CO_2. The large pool of C in the soil is vulnerable to climatic warming and its potential loss may amplify further warming (Cox et al., 2000). However, current predictions are based on empirical models because there is a general lack of knowledge about the mechanisms that influence decomposition of SOM. Among the factors affecting SOM decomposition, temperature, soil moisture and C input are perhaps the most important.

Global temperatures are expected to rise significantly during the 21st century and beyond (IPCC 2007). Different hypotheses can be used to predict the potential dynamics of soil C stocks in such a changing environment (Gartener et al., 2004). The effects of climate change due to elevated atmospheric CO_2 concentrations on soil C dynamics causing a positive and/or negative feedback to climate change. Decomposition of soil organic matter is more sensitive to temperature change than the NPP (Gartener and Cardon, 2004), consequently increasing

temperatures will result in a net transfer of soil C to the atmosphere as soil organic matter (SOM) decomposition is stimulate more than net primary productivity (NPP) (Kirschbaum 2000). This would lead to a positive feedback mechanism: the release of soil C further increases atmospheric CO_2 concentrations, leading to even higher surface temperature and consequently more C loss through accelerated decomposition (Cox et al., 2000). However, there is also a potential inhibition to this positive feedback. Increase decomposition rate may stimulate greater soil nitrogen (N) availability leading to higher NPP, which potentially increase C input into soil through litter fall and rhizodeposition that would somewhat offset the increased soil C loss. Therefore, soil C dynamics depend on the soil C balance changes. Land use change alters soil C and induced nitrogen due to fertilization from agricultural fertilizer usage and the combustion of fossil fuel by producing predominantly NH_3 and (NO_3) to NO (NO+ NO_2), eventually leading to dry and wet N deposition on vegetation and soil (Galloway and Cowling, 2002). Soil C stocks gain more C than they lose due to rising temperatures in N rich environment. Increase soil N availability will increase NPP and subsequently litter and thus soil C inputs. Furthermore, higher N content might stimulate initial litter decomposition and latter suppressing humus decay (Jandl et al., 2007), thus leading to stabilisation of SOM in mineral-associated fractions (Neff et al., 2002). Consequently, more humus formation occurs with litter of higher N content or low C/N ratio (Berg and Meentemeyer, 2002). Obviously, other factors co-exist and also impact on soil C stocks. However, temperature seems to play a key role environmental factor (Rodeghiero and Cescatti, 2005).

1.4 SOIL RESPIRATION IN MEDITERRANEAN ECOSYSTEMS

Over one half of the area worldwide with Mediterranean-type climate is located in the Mediterranean Sea basin and embraces parts of three continents: Europe, Asia, and Africa (Lulla 1987); hence, the commonly used name for the climate type. This climate and the associated biome occur in four other limited and widely scattered areas of the world: the Pacific Coast of North America from southern Oregon to northern Baja California; parts of West and of South Australia; the central Chilean coast, and the south-western Cape region of South Africa. Woodland ecosystems cover an area of 17 x 10^6 Km^2 of the earth's surface, occupy less than 5 % of the global land surface (Cowling et al., 1996), and contain 15 % of annual C sink (Taylor and Lloyd, 1992), and second to tropical forests in their contribution to the earth's terrestrial primary production (Burton et al., 2002; Atjay et al., 1987). On the African continent, Mediterranean woodland is not as extensive as other biomes (Scurlock and Hall, 1998; Scurlock et al., 2002). But despite the importance of MTE's in the global C cycling, little is known about

R_S (C sources and sinks), especially as these systems are increasingly degraded and invaded in both terrestrial and riparian environments.

Soil respiration varies with different ecosystem-types, reflecting intrinsic characteristics of those ecosystems in prevailing environments and biological activities (Bond-Lamberty and Thomson, 2010; Jeffre et a., 2007). CO_2 exchange of MTE's is out of phase with the seasonal pattern of C exchange in temperate forests (Reichstein et al., 2002). The usually prolonged summer drought limits gas exchange (Reichstein et al., 2002; Eamus et al., 2001), but rainfall is abundant during the winter, so the plants are physiologically active when temperatures are cooler, days are shorter, and less sunlight is available than in summer. Consequently, MTE's have less potential to acquire C than temperate systems that are active during the warmer and brighter summer. In certain Mediterranean climate regions, grasslands consist mainly of annual grasses that are active during winter and spring growing season and use C_3 photosynthetic pathway. On the contrary, grasslands in temperate continental regions are perennial and physiologically active during summer growing season. Nevertheless, photosynthetic pathways, C_3 and C_4 grass species coexist, and favored much more toward C_4 species.

Overall, factors such as precipitation are often important to predict the regional variability in R_S (Epstein et al., 2002). Another prominent feature of MTE's is the effect of episodic rain on R_S during the summer (Reichstein et al., 2002b; Rey et al., 2002; Baldocchi 2003). Two mechanisms may produce enhanced respiration rates after rainfall. One is a physical dislocation of soil air and CO_2 by the downward-moving front of water in the soil. But this effect is short-lived, and the volume of air in the soil profile is relatively small. The other mechanism is rapid activation of heterotrophic respiration (Birch 1958). Still, little is known about the effects of these supplementary precipitation sources on R_S processes (Jacobs et al., 2002). Furthermore, the mechanism of root adaptation to water stress is of great value as it help plants to overcome drought such as extracting water from deeper soil horizon. Root respiration decrease during drought period (Bryla et al., 2001) consequently root water content decrease with a subsequent reduction in root cell pressure leading to cell death and lower root respiration. Root resistance to water stress varies among species and among different root system from the same individual (Korhonen et al., 2009; Palta et al., 2005; Nobel and Paltta, 1989; Nobel 1998, 2005) and excess of water content in soil reduce root growth, mainly by decreasing the availability of oxygen.

1.5 CARBON TURNOVER AT THE LANDSCAPE SCALE

Given the broad range of landscape elements that can exist within a particular watershed, and owing to the different responses that CO_2 efflux can respond to different meteorological (precipitation, seasonal drying of the soil, temperature) conditions, it is important to determine the overarching control on soil CO_2 efflux across riparian ecosystems. Soil respiration at landscape level is organized by physical structure and associated biotic communities and can respond to different and opposing controls (Pacific et al., 2009, 2010b). Previous study has examined the spatial variability of R_S across landscapes and has revealed important differences in CO_2 efflux associated with spatial location (e.g. Pacific et al., 2008). For example, significant differences in R_S have been found between two different landscape positions associated with a riparian zone in Tuscany, Italy (King et al., 2004). In another case, in an agricultural landscape, Tufekcioglu et al. (2001) found that riparian zone have higher R_S compared to adjoining, but higher elevation, croplands. Therefore, it is important to understand and consider the role of landscape position and biophysical gradients as drivers of R_S in these riparian landscapes (Pacific et al., 2008).

Different physical processes may be operating in different landscape positions, which affect soil CO_2 efflux rates. McCarthy and Brown (2006) found that soil CO_2 efflux in dry upland soil was limited by low soil gas production despite high soil gas diffusivity, resulting in similar CO_2 efflux compared to riparian zones. An increase in soil moisture often leads to higher soil CO_2 production, but can at the same time decrease soil gas transport (Washington et al., 1994; Moldrup et al., 2001). Surface CO_2 efflux in riparian areas is limited by low soil gas transport despite high CO_2 concentration, whereas CO_2 efflux in dry upland areas can be limited by low soil gas production despite high soil gas diffusivity (Pacific et al., 2008). Sotta et al. (2006) also found similar CO_2 efflux across lowland and upland positions. Landscape attributes such as wet, dry and upland slopes impacted groundwater table dynamics and affected soil respiration and driving variables (Pacific et al., 2010). However, higher soil water content and higher and more persistent groundwater tables may lead to significant differences in R_S as function of landscape position. This variability in soil moisture can in turn affect other factors participating in CO_2 production, such as differences in plant above-and belowground biomass, and the abundance of SOM (Sjogersten et al., 2006; Reinecke et al., 2008a) as well as the magnitude of soil diffusivity (Sotta et al., 2007; Moldrup et al., 2001). Vegetation is major aspect of variability that can also influence R_S at the landscape level due to differences in root respiration and quality and quantity of litter (Raich and Tufekcioglu, 2000; Pacific et al., 2008). These biophysical

gradients across landscape positions can lead to strong spatial heterogeneity in R_S. Investigating and quantifying seasonal R_S and the basic role of landscape in natural, invaded and cleared riparian zones in soil CO_2 production and differences in the drives of R_S will add value to our understanding of landscape-scale C dynamics.

Riparian zones are landscape features exposed to high levels of disturbance, and thus also have high levels of special variability within it. Riparian ecotones are two dimensional transitional zones of direct interaction between the terrestrial uplands and the aquatic ecosystems extending from the edge of the water bodies to the edge of the terrestrial uplands (Naiman and Décamps, 1997). Riparian and terrestrial zones are two dominant landscape elements in catchments and generally have distinct soil water content and groundwater table regimes (Naiman and Décamp, 1997; Pacific et al., 2008), leading to differences in soil and vegetation characteristics (McGlynn and Seibert, 2003; Pacific et al., 2008). The riparian area often supports diverse and productive plant communities. Variable topography, hydrology, and soils result in a wide range of physical habitats within close proximity, each supporting distinct plant species. The size of riparian zones ranges from narrow strips in constrained headwaters, with the few geomorphic features, to complex systems along rivers characterized by physically diverse floodplains as well as by hydromorphic soils (Phillips et al., 2001; Mourier et al., 2008; Naiman and Décamp, 1997).

Riparian habitats range from bare sediment surfaces with extreme thermal variation and high water stress and therefore low productivity, to environments rich in resources that sustain high productivity, such as vegetated island and riparian forest (Naiman et al., 2005; Tockner et al., 2006a) with repeated rejuvenation of habitat patches of different ages and successional stages. However, the vegetation in riparian ecosystems of Mediterranean-type climates is typically sclerophyllous and evergreen, adapted to water stress during the dry summer period, and able to grow on infertile soils (Herrera 1995; Maamri et al., 1994; Stewart and Davies, 1990; Britton 1990; Jacobs et al., 2007). In the South African Mediterranean-climate region, the fynbos, even finer gradients are apparent, with near stream zones consisting of herbaceous, hydrophytic vegetation, whereas slightly higher elevation riparian areas with lower inundation frequencies have more shrubby or woody plant assemblages (Reinecke et al., 2008b). Terrestrial areas in the fynbos are dominated by sclerophyllous woody vegetation of low stature, which is fire adapted, whereas riparian areas are generally less prone to fires (Cowling and Holmes, 1992).

The availability of year-round moisture near streams enables deciduous woody vegetation to occur in the riparian zone as seen in Mediterranean-type streams in the Northern Hemisphere (Holstein 1984), with equivalent species assemblages occurring in some Mediterranean regions (Shmida 1981). With increasing aridity, the riparian vegetation becomes shorter, more scattered, more restricted to the side of the active channel, and markedly different from the upland regions (Fisher 1995; Maamri et al., 1994). In these riparian zones, riparian vegetation is also related to site-specific attributes such as elevation, slope, and lithology (Faber et al., 1989; Minshall et al., 1983); it may thus exhibit spatial variability in R_S and factors that might control R_S. The availability of SOM and density of plant roots, which provide the substrates for soil biological activity, may control the overall magnitudes of R_S (Franzluebbers et al., 1996, 2001; Kelting et al., 1998). Although riparian vegetation of humid regions cannot withstand even mild fires (Naiman et al., 1998), vegetation along riparian streams is frequently exposed to natural and human-made fires (Britton et al., 1993; Britton 1990; Specht 1981; Trabaud 1981) and therefore may be more fire-adapted and show more rapid recovery after fire. These factors affect plant biomass, litter quality, litterfall rates, and soil organic matter stocks, thus also R_S.

Fire effects on ecosystems are related to frequency, intensity and timing of occurrence which are in turn, affected by climate conditions, vegetation type, fuel loads and landscape morphology (Pyne et al., 1996). Fire is known to impact the belowground species composition including organic matter content of the soil, along with N-mineralization rates, and total N, soil temperature, and pH (DeBano 1998). Studies on trees harvest have shown high, low, and no changes in R_S rates but soil moisture decreased by 20 % due to fire effect (Edwards and Ross-Todd, 1983; Weber 1990; Tang et al., 2005). However, fire can be mitigated a year-to-year reduction in soil temperature (Kobziar and Stephens, 2006), depending on treatment and fire intensity as well as site, since disturbance effects are site dependent. Andersson et al. (2004) field experiment in the Africa savanna woodland demonstrated that the low severity fire indirectly stimulated C microbial and may be potential denitrification for enzyme activity. In contrast, when the fuel load was doubled, a direct adverse effect on C microbial was shown and the fire-induced stimulation of potential denitrification enzyme activity was less pronounced.

Ecosystem functioning and geomorphology is necessary to river biodiversity since the channel pattern provides habitat for the biota and a physical framework for ecosystem processes. Maintaining natural stream flow regimes are critical to conserving the integrity of riverine ecosystems (Poff 1997). Intensive land use such as road construction, power line construction, clearing of forests for agriculture, and urbanization increases hydrological extremes resulting in

profound changes in landscape composition and structures and can impact plant and animal community properties (Debinski and Holt, 2000), hence also factor that may influence R_S such as water availability and temperature. For instance, harvesting introduces a considerable amount of area-of-edge where and animal species composition (Haefner et al., 1991), microclimate (Zheng et al., 2000) and ecosystem processes can undergo dramatic changes (Laurance et al., 1997). Land-use can influence both riparian and upland areas by affecting landscape R_S rates but at different magnitudes (e.g. soil temperature and changes within landscape) (Zheng et al., 2005), suggesting that, spatial variation in land cover composition can significantly affect R_S at the landscape level.

Up to 60 % of all the world's rivers are currently impounded (Nilsson end Berggren, 2007). Hydrological variable due to highly processing of organic matter in semi-arid lowland rivers may be even more complex (Allison et al., 2010; Thoms and Sheldon, 2000). Conversely, about two thirds of the freshwater flowing to the oceans is estimated to be controlled by dams (Naiman et al., 1993), and 85 of the 139 largest river systems, or 77 % of the flow from the rest of the world river, are moderately or strongly affected by regulation (Dynesius and Nilsson, 1994). Soils and sediments are the major global reservoirs for C in the form of organic matter. Dispersal of plant by water, or hydrochory, is important in structuring riparian plant communities along rivers (Nilsson et al., 1991b; Johansson and Nilsson, 1993, Johansson et al., 1996; Freckman et al., 1997), but is obstructed by agricultural development.

Dams are barriers for aquatic diaspores, and the reservoir surfaces between dams tend to be effective traps, since diaspores are likely to be washed ashore by wind and wave action. Their multiple purposes such as sediment and soil erosion control, water supply and regulation, groundwater recharge, and agricultural production, they are actually human introduced multifunctional landscape units. Study by Lü et al. (2012) indicated that dams had retained about 42.3 million tons of SOM carbon with a high spatial variability. This is a significant amount similar to about 1.48 % of the soil organic matter stored in the 0-40 cm soil layer or roughly 4 % of the estimated C emission from fossil fuel in China in 2000. Furthermore, flood pulses, which are the major events for hydrochory in free-flowing rivers (Nilsson et al., 1991b; Thorp and Delong, 1994; Schneider and Sharitz, 1988), are reduced or absent. Conversion of natural vegetation to agriculture is the most frequent land-use in the riparian zones. The advent of irrigation allowed large areas of upland shrub communities within riparian zone hydrology to be determined as flow path influencing both the extent of contact between nitrate and organic matter and the residence time of the nitrate plume in the C rich zone (Rassam et al., 2005). Hill

(1996) and Burt et al. (1999) found that riparian nitrate removal have tended to focus on sites with similar hydrogeological setting where flow paths are shallow, often restricted by impermeable clay layers and flow direction is from upland areas to surface water (Hill 1996, 2004). Observed riparian zones showed large potential for denitrification, nitrate still passed through the zone via springs and gravel lenses beneath the floodplain soil. Damming can cause increased turbidity and sedimentation in streams resulting from the removal of soil disturbance, and soil rutting. Fuel spills and chemical cleaning of building materials have the potential to create pollution. The carbon retention effects due to dam construction are parallel and synergistic to their effects on sediment trapping during soil erosion and sediment transport processes, which have been largely neglected.

1.6 ALIEN INVASIVE PLANTS AND SOIL RESPIRATION

The invasion of exotic plants is one of the main causes of land cover change, of biodiversity loss, and of other changes in ecosystem structure and function (Koteen et al., 2011), and their introductions (Hodkinson and Thompson, 1997; Mack et al., 2000; Walther et al., 2009; Parmesan and Yohe, 2003) have resulted in biological invasions, which can have profound effects on the riparian habitats and the biodiversity therein (Vitousek et al., 1997). Invasive leguminous trees like *Acacia* species from Australia, *Acacia manguim* in eastern Amazonia (Verchot et al., 2008), and Vitousek (2004) in Hawaii have become problematic in many ecosystems around the world (Marchante et al., 2007; Dye and Jarmain, 2004). In South Africa, *Acacia mearnsii* has been recognized as a major threat to water supply in the Mediterranean-climate fynbos biome. The invasiveness of this genus is partly due to its ability to produce large amounts of long-lived seeds and the development of a large crown (Galatowitsch and Richardson, 2005). Its leaves and branches may also have allelopathic properties (Jeffrey et al., 2010; Callaway et al., 2008). Due to the increase in the height and biomass of vegetation *Acacia mearnsii* infestations increase rainfall interception and transpiration rates, which causes a decrease in stream flow (Dye and Jarmain, 2004)? Soil under *Acacia* species becomes desiccated more quickly than it does under natural vegetation. *Acacia mearnsii* and *Acacia longifolia* stands also destabilize stream banks and support a lower diversity of species (Richardson and Rejmánek, 2011; Sankaran 2002; Le Maitre et al., 1996).

Invasive plants alter biogeochemical cycles by changing nutrient mineralization rates, soil and water chemistry, and nutrient immobilization. Invasive plants increase aboveground biomass and decrease litter quality and leads to an increase in net soil C pools and N mineralization

within sites (Evans et al., 2001; Mack et al., 2001; Agren and Knecht, 2001). Gaseous emissions from terrestrial ecosystems are exacerbated by soil degradation, of which the effects of exotic plants and soil erosion are the most predominant form in MTE's climate. Change in the composition of plant species induced by the degradation of ecosystems may alter soil respiration rates and C sequestration (Stock et al., 1995). Furthermore, few studies have specifically investigated the effects of invasive alien plants on nutrient cycling and mineralization (Marchante et al., 2007; Stock and Allsop, 1992; Vitousek and Sanford, 1986) and ecological impacts (Richardson and Van Wilgen, 2004) but the impact on soil respiration and soil CO_2 production remain sparse and poorly understood. IAPs affect the availability of other resources such as soil nutrients, water, and light, and could also alter fire regimes and enhance CO_2 production (Shackleton et al., 2011; Field et al., 1997; Evrendilek et al., 2008). However, IAPs alter R_S (Marchante et al., 2008), and have negative effects on the ecosystem (Yelenik et al., 2004), because high temperatures may favour the photosynthesis pathway of plant species; climate change may counteract these consequences of increasing CO_2 concentration. Yelenik et al. (2004) also found that the impact of the alien N_2-fixing plants stems from higher litterfall rates which coupled with higher N concentrations, results in more N being returned from the aboveground biomass to the soil. These increased levels of organic matter and soil total N under acacia stands would lead to consistently higher levels of available inorganic N than in native fynbos biome where ion exchange resin N availability remained low and relatively constant throughout the year. Whereas exotic species may benefit from higher CO_2 concentration in some regions, native also may benefit in others. Plants with certain CO_2 responsive traits are likely to take advantage of these rises in CO_2 flux, especially if they are growing in an environment where those traits are rare. For example, *Acacia* spp. growing in C_3 species dominated ecosystems is likely to benefit from the rise in CO_2 concentration. However, Dukes (2000) stated that, leguminous shrubs might become especially invasive as rising CO_2 concentration in the atmosphere stimulates N fixation.

Yelenik et al. (2004) found that the effect of an N-fixing invader, *Acacia saligna*, on Sand Plain Fynbos was to increase biomass production and litterfall and decomposition rates. Soils from *Acacia* invasion had a higher N concentration, with no concentration difference between infested and cleared *Acacia* sites. These species increased nitrogen cycling rates within the low-nutrient and decrease soil pH in soil environment of fynbos. Musil (1993) reported that riparian habitats are particularly sensitive to invasion and *Acacias* are better at regenerating after a fire than are native fynbos species (Musil 1993).

However, Blank et al. (2003) study revealed that, high water tables in riparian zones can reduce fire effect on nutrients with loss of C and N during fires reduced on sites with high water tables compared with low water table areas. Invaded ecosystem areas accumulated higher litter densities with greater N contents and lower C/N ratio than native riparian zones, higher potential rates of nitrification in the *Acacia* soils (Scharfy et al., 2009). In terrestrial forests, R_S increases with aboveground primary production that reflects the importance of plant productivity and allocation to roots, microbial symbionts and roots exudates in determining R_S (Högberg et al., 2001; Ruess et al., 2003). It is well known that the rate of litter decomposition is higher with species such as *Acacia mearnsii* which are considered to be related to the C/N ratio in invaded ecosystems (Takeda 1994). With lower C/N litter of alien spices are generally easily attacked by microorganisms as nitrogen-rich. In contrast, native species usually have higher ratio of C/N in leaf litters, which is hardly decomposed by microorganisms because many phenolic compounds, especially high content of lignin prevents it from being digested. However, the range of C/N ratio seems to be the parameter most revealing in terms of nitrogen mineralization limited by the availability of carbon (Scharfy et al., 2009; Yuko et al., 2006). Earlier studies demonstrated invasive alien plants to influence inputs of C and N, and microbial processes as well as altering ecosystem levels characteristic in the Western Cape (MTE's) region (Yelenik et al., 2004; Ashton et al., 2005; Petsikos et al., 2007). Up to date, research has not established a link between invasive alien plants (IAPs) and clearing of riparian zones and R_S in the environment. Within these categories, it's still difficult to predict which variable will influence soil respiration the most. However, knowledge about R_S at landscape levels can lead to the identification of factors that will confer the impact of IAPs as well as the response to CO_2 production in degraded riparian ecosystems. Invasion has the potential to substantially reduce soil C storage on a regional scale (Bohlen et al., 2004). There is great need to characterize the nature and extent of these invasions, their effects on soil C dynamics, and their interaction with climate change. C_4 plants use nitrogen more efficiently so can out-compete C_3 plants in an undisturbed ecosystem. However, global change is likely to change this competitive balance (Dukes 2000). Vegetation clearing, agriculture practices and increases in atmospheric nitrogen all increase nitrogen availability in the soil, giving C_3 plants an advantage over C_4 plants. Furthermore, an increase in atmospheric CO_2 will improve nitrogen-use efficiency of C_3 photosynthetic pathways, giving them an even greater advantage over C_4 plants (Milton 2004; Dukes 2000). These anthropogenic changes may result in increased biomass of invasive leguminous trees in riparian zones in future, which would influence the organic matter composition of riparian soils, and thus also R_S.

1.7 STUDY AREAS

Selected study areas were located around Stellenbosch town and in the vicinity of the south-western cape region. The study areas include the Eerste River at Jonkershoek and it has it sources in the Dwarsberg Mountains 1320 m altitude (Figure 1.2). Although all the river systems show some anthropogenic disturbances such as dams, water extraction point (Figure 1.4A and B), and other modifications this was deemed unavoidable and most of the sites are located above these disturbances. All the reference sites fall within Eerste River and Dwars River catchments. An invaded site (a mixture of *A. longifolia* and *A. mearnsii*) was positioned downstream from the natural site in the Dwars River catchment. The Wit River site (invaded) runs along Bainskloof pass and is situated in the mountain stream transitional zone and alien clearance is still ongoing throughout the riparian zone (above my site), with densest invasions found in the lower sections of the river (where the site is located Figure A3.1). The Molenaars River site (cleared) is located at DuToitskloof and another invaded site was located near the small town of Rawsonville before joining the Breede River. Alien clearance is evident throughout the river and is on-going; however the invaded site was established in the lower part of the river (lower Molenaars: invaded) with a cleared site 2km upstream (upper Molenaars: cleared). The Molenaars River main channel is fairly braided in sections with islands along much of its length. These islands are relatively close to either side of the river and become more apparent in the summer seasons with the decline of water levels, becoming partially submerged for much of winter season. The Jakkals River falls in the private property of Beaumont Wine Farm areas (lower Jakkals: invaded), and the cleared site upstream in the Jakkals Mountain. Another cleared site was in the lower foothills section of the Sir Lowry's River, on the farm Wedderville Estate (Table 1.1). Site information and selection were partially based on a previous study by Reinecke and King (2007), together with personnel communication from land owners and nature reserve managers.

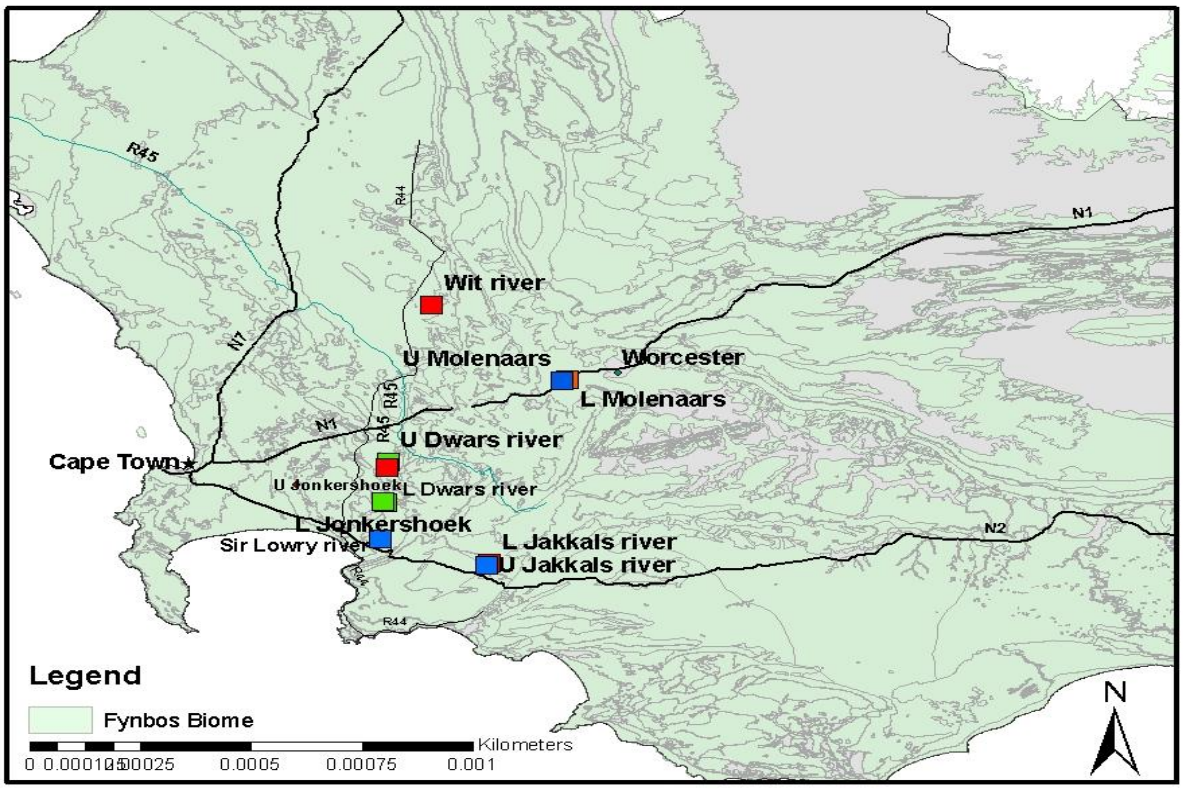

Figure 0.2: Study site within six river systems in the Western Cape, South Africa. Natural sites are indicated in green, invaded sites in blue, and cleared in red. Map created with spatial data provided by the South Africa National Biodiversity Institute (SANBI).

1.8 PROBLEM STATEMENT

Changes in the composition of plant species induced by degradation of riparian ecotones IAPs may alter R_S rates and C sequestration in the ecosystem (Stock et al., 1995). Gaseous emissions from terrestrial ecosystems are exacerbated by soil degradation, of which accelerated exotic plant introductions and soil erosion is the most predominant and widespread form in Mediterranean-type climate. Yet the research information is extremely scarce on soil C dynamics in relation to soil degradation in general and the relationship between R_S and IAP_S in particular. The steady state equilibrium of the soil organic C (SOC) pool in undisturbed ecosystems is drastically disturbed by anthropogenic activities attendant upon conversion of natural to agricultural ecosystems. However, it is recognized increasingly that restoration of ecological processes, such as nutrient turnover or hydrological flux, may be critical components of restoration outcomes. This understanding has been paralleled by an upsurge in ecological research on the linkage between ecological structure (e.g., species diversity, habitat complexity) and ecological function (e.g., biogeochemical processes, disturbance regimes) (Falk et al., 2006).

Despite the importance of R_S in the C budget at various and temporal scales, numerous ecosystem and global-level studies on R_S (Pacific et al., 2009; Ma et al., 2007; Raich et al., 2002; Ma et al., 2004; Howard and Howard, 1993; Lloyd and Taylor, 1994), little effort have been made to understand how changes in soil moisture, temperature and land degradation could affect R_S rates at the landscape level. Studies on the interactions between seasonal R_S and alien invasion in riparian landscapes are even rarer (Jauhiainen et al., 2012; Nouvellon et al., 2012). Studies pertaining to differences in seasonal R_S rates among the various riparian areas that comprise invaded and restored riparian ecotones can provide information to land managers, helping them to understand how riparian R_S is altered by IAPs disturbance such as *Acacia* spp. and removal of invading trees in the population of pristine fynbos plants under climate change scenarios. This study measured seasonal R_S in riparian ecosystems and how selected biophysical and hydrological controls influence soil CO_2 efflux in a topographically complex area along mountain stream transitional and foothill riparian zones.

1.9 HYPOTHESES AND RESEARCH QUESTIONS

Specifically the aims of this study were to address the following key questions:

(i) How does R_S in riparian ecotones differ from upland areas, and amongst natural, invaded, and cleared riparian transects?

(ii) What is the role of riparian R_S in the regulation and return of C stocks to pre-invasion levels?

(iii) What are the relationship between the biophysical, biogeochemical and hydrological characteristics of soil (riparian) and R_S?

(iv) What are the most influential characteristics of R_S at landscape level?

(v) How does potential soil respiration (PR_S) relate to in-situ respiratory rates?

1.10 THESIS STRUCTURE

This thesis is structured in the following menner:

- Chapter 1 presents a basic introduction and a comprehensive review of R_S based on various independent sources of reference as well as study areas and focus of the study.
- Chapter 2 describes the methods used and the results obtained from measurements of R_S conducted "*in situ*" at the sites covering natural, invaded and cleared riparian zones.
- Chapter 3 unpacks the methods used for assessing potential R_S "*ex situ"* during incubation processes and results of the incubations.

- Chapter 4 summarizes the key findings of each data chapter, and also integrates the new knowledge to investigate how R_S. Changes with invasion and clearing, and what factors control R_S. Under different conditions of degradation and restoration.

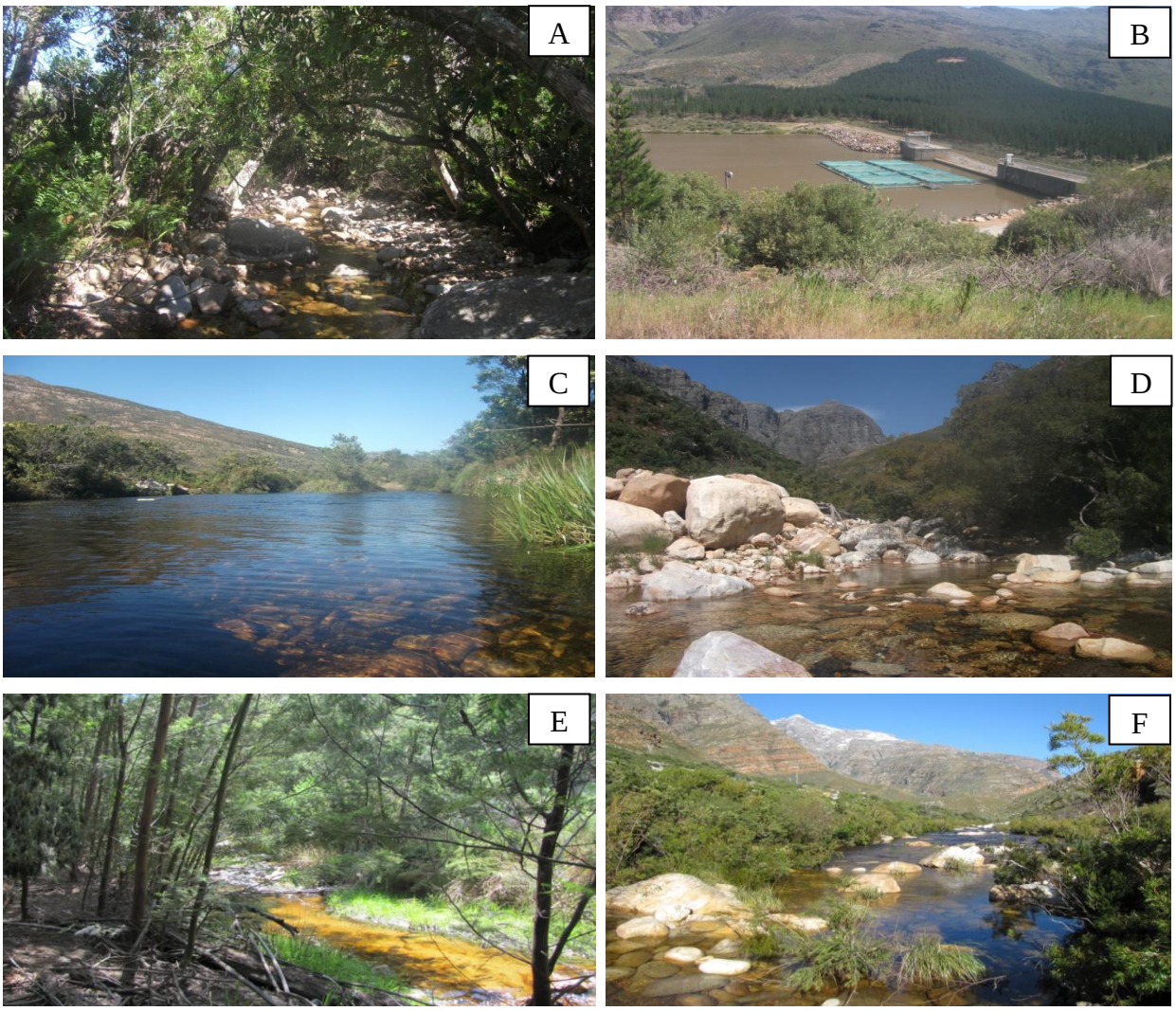

Figure 0.3: Location, typical riparian zones study site topography and vegetation type around the River system in south-western Cape. Top-down view of study areas (sites) and river systems of native at Jonkershoek (A and B), the Wit River system in Bainskloof (C), Dwars river system in Kyremore (D), bottom (right) picture showing an invaded site, occupied by exotic trees, the Australian Acacia spp. at lower Jakkals river system (E), and the cleared site (left) at upper Molenaars near Rawsonville Town in DuToitskloof (F).

Table 0.1: Geomorphological characteristics and site-specific information on each of the study sites within the south-western Cape region.

Sites	Geology	Invasion Status	Coordinates	Landowners	History of invasion	History of clearing	Fire History	Gradient	Longitudinal zone
Upper Eerste River	Sandstone/Granite	Natural	33°57'13.6" S; 18°58 '43.8" E	CapeNature	No evidence	None	Burned in March 2009	0.038	Mountain Stream Transition
Lower Eerste River	Sandstone/Granite	Natural	33°59'22.28"S; 18°58'03.17"E	CapeNature	No evidence	None	Burned in March 2009	0.058	Mountain Stream
Upper Dwars River	Sandstone/Granite	Natural	33°57'16.04"S; 18°58'47.78"E	CapeNature	No evidence	None	Burned in March 2009	0.120	Mountain Headwater Stream
Wit River	Sandstone/Granite	Invaded	33°32'18.5" S; 19° 0'55.6" E	Mount Bain Development	Invaded for ≥ 15 years *Acacia mearnsii*	No evidence	No evidence of recent fire	0.022	Mountain Stream Transition
Lower Molenaars	Sandstone	Invaded	33°42'16.95"S; 19°13'59.42"E	CapeNature	Invaded for > 10 years A. *mearnsii* /A. *Longifolia*	Cleared in summer 2011	Burned in March 2011	0.020	Mountain Stream Transition

Lower Jakkals River	Sandstone	Invaded	33°12'31.81"S; 19°10'38.75" E	Beaumont Wine Farm, Bot River	Invaded for > 15 years A. *mearnsii* /*A. Longifolia*	Yes, some evidence	No evidence of recent fire	0.050	Mountain Stream
Lower Dwars River	Sandstone/Granite	Invaded	33°56’5336”S; 19 58’11.25”E	CapeNature	Invaded for > 10 *years A. mearnsii* /*A. Longifolia*	No evidence	No evidence of recent fire	0.050	Mountain Stream
Sir Lowry’s River	Sandstone/Granite	Cleared	34°05'41.5"S; 18°56'39.7"E	Wedderville Estate, Sir Lowry Village	Mixed invasions: *Acacia spp*.+ *Pinus* spp.>8 years ago	Cleared in 2002 and annual fooled up by landowner: fell and burn	No evidence of recent fire	0.068	Mountain Stream

Upper Molenaars	Sandstone	Cleared	33°42'38.56"S; 19°11'49.24"E	CapeNature	Invaded for >7 years mostly *Acacia mearnsii*	Yes. Initial treatment: 2002-2003 follow-up treatments clearing treatment: fell and remove	No evidence of recent fire	0.044	Mountain Stream
Upper Jakkals	Sandstone	Cleared	33°13'01.10"S; 19°12'25.84"E	CapeNature	A. mearnsii/A. Longifolia > 12 years	Initial clearance: 1996-97. 2follow-up treatments. Treatment: fell and burn	Burned in January 2010	0.040	Mountain Stream

Information was gathered from local conservation agencies, farm managers and owners.

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CHAPTER 2

TOTAL SOIL RESPIRATION IN FYNBOS RIPARIAN ECOTONES: THE INFLUENCE OF LANDSCAPE POSITION AND *ACACIA*-INVASION STATUS

2.1 ABSTRACT

Acacia mearnsii, *Acacia longifolia*, and *Acacia dealbata* are among the most widespread invasive alien plants (IAPs) in South Africa and are often located within riparian catchments with extensive woody stands that dominate riparian areas. These invasions may be significant to the overall riparian carbon cycling as soils are often high in soil organic matter, low C/N ratio, and elevated biological productivity due to the availability of nutrients and water within riparian ecosystems. This chapter explored seasonal soil respiration in degraded riparian ecotones of the south-western Cape, South Africa. Soil respiration measurements were conducted in selected riparian ecosystems in the Mediterranean type region of the Western Cape, South Africa, with differing invasion status: natural, invaded, and cleared riparian ecosystems. Soil respiration at all riparian sites showed pronounced seasonality with highest and lowest values observed during the dry and the wet season. On average, highest and lowest soil CO_2 effluxes between invasion statuses were found at invaded riparian sites with R_S rates of 5.65µmol m^{-2} s^{-1}, and lowest values of 2.89 µmol m^{-2} s^{-1} at natural, and 2.53 µmol m^{-2} s^{-1} at the cleared riparian sites during summer. Overall, Soil respiration was highest in the riparian zones and lowest in the terrestrial adjacent uplands fynbos in summer 2011 with R_S value of 7.34 µmol m^{-2} s^{-1} in the dry bank. The results also indicate that soil CO_2 efflux of these ecosystems are driven by different biophysical factors depending on the season, with soil moisture limiting R_S during the summer. Soil water content alone was a poor indicator of R_S while a combination of both factors provided a stronger relationship with R_S at $P < 0.05$. When *Acacia* individuals are removed from riparian dry banks, R_S declines significantly, such that rates resemble those in natural riparian ecotones, suggesting a restoration of ecosystem functioning, at least insofar carbon cycling is concerned. Our finding add to the small body of measurements of carbon cycling in South Africa and make a useful contribution in understanding carbon dynamics of the invaded riparian ecosystems in Mediterranean type areas.

KEYWORDS: Mediterranean ecosystem; invasive alien plants; natural; invaded; cleared; CO_2 efflux; soil temperature; soil water content; terrestrial

2.2 INTRODUCTION

Soil respiration measurements, which integrate root respiration and microbial activity, have been carried out in many different ecosystems (Pacific et al., 2010; Tang and Baldocchi, 2005; Liu and Li, 2005; Raich et al., 2002; Raich and Tufekcioglu et al., 2001). Soil respiration is derived from two principal sources known as autotrophic respiration by roots and associated mycorrhizae, and heterotrophic respiration by microorganisms that decompose leaf litter and soil organic matter. Soil respiration (autotrophic and heterotrophic combined) accounts for half the CO_2 flux from terrestrial ecosystems to the atmosphere annually (Amthor 1995; Schlesinger 1997; Thuille et al., 2000). The significance of soil CO_2 efflux measurements is that it indicate the amount of C returned to the atmosphere via the soil surface, and it also act as an index of belowground processes and C cycling capacity of soil ecosystems (Raich et al., 2002; Mielnik and Dugus, 2000).

Mediterranean ecosystems (MTE's) have dry warm summers and wet and cool winters, two predictable climatic extremes that places a certain amount of stress on native plant and animal species (Aschmann 1973; Gasith and Resh, 1999). In general, productivity levels in these ecosystems tend to be low, plant species have adapted their lifestyles to take advantage of windows of opportunity that will allow maximum productivity, e.g. highest productivity in spring, and early summer, while many plants are not able to be very productive at the end of summer when it is very dry (Stock and Allsopp, 1992). In the Cape Region and Australia soils are generally old and nutrient poor (Lambers et al., 2008a); this is less true for the Mediterranean and the Californian Biogeographic Province.

Some of the adaptations of plants to the poor soils include Proteoid roots and ericoid mycorrhiza, however, vegetation tend to be low shrubs and bulbs, especially in the Cape. Plant leaves are generally sclerophyllous, though the main reason for this remains unclear, some consider it an adaptation to the seasonal drought, while others suggest it may be an adaptation to the low soils nutrient levels (Mitchell et al., 1986; Witkowski 1991; Yelenik et al., 2004). Due to the poor soils, litter quality tends to also be low, which means that litter decomposition rates are also low. These regions are almost without exception considered hotspots for biodiversity, but are also heavily populated by people, and heavily modified for agriculture, which makes

understanding the ecology and ecosystems of Mediterranean regions critical (Cowling and Heijnis, 2001; Cowling et al., 2004). Few studies have been carried out to understand the links between Mediterranean plant traits and soil respiration or between soil properties and soils respiration in MTE's.

Soil respiration in MTE's show a distinct seasonal cycle, with higher R_S during warmer months, but generally low rates compared to other biomes, such as tropical rainforest ecosystems and some mesic environments (Benjamin 2006; Luo and Zhou, 2006). The responses to manipulate R_S to precipitation in these regions (MTE's) vary with season and years, depending on the amount of precipitation (Asensio et al., 2007; Chou et al., 2008). In addition to being controlled by climatic variables, R_S is regulated by biotic factors such as vegetation (Ryan and Law, 2005; Jauhiainen et al., 2005; Wan et al., 2007). Heterogeneous ecosystems, e.g. Mediterranean are comprised of relatively distinct patches, such as sites dominated by shrubs and open intershrub gaps dominated by herbaceous vegetation. Shrub landscapes are often rich in resources, patches as those places dominated by shrubs and open intershrub dominate by herbaceous vegetation. They are also rich in resources, such as water and nutrients, and are therefore called islands of fertility (Schade and Hobbie, 2005). Differences between landscapes affect root and microbial activities, the main sources of CO_2 in R_S tract. Shrublands offer the possibility to study the effect vegetation on R_S by comparing microsite landscape responses to changes in rainfall. Studies have so far shown that episodic rainfall in summer increased R_S at landscape with shrub patches to a great extent than intershrub open areas (Zheng et al., 2005; McCulley et al., 2007; Potts et al., 2008). To predict responses of the C cycle to climate change in dry ecosystems, heterogeneous effects of changes in precipitation on CO_2 effluxes must be at understood at landscape level on annual basis.

Due to the history of occupation, the population density, the role of agriculture in ecosystem modification and international trade, MTE's are all highly invaded by a multitude of exotic plants, animal and microorganisms (Cowling et al., 1992; Mucina and Rutherford, 2006). Especially problematic in all the Mediterranean environments are plants adapted to these climatic zones that become invasive in Mediterranean ecosystems where they are new introductions. In South Africa, *Acacia* species from Australia have become invasive, after introduction due to various commercial reasons, and as many of them originated in Mediterranean Australia, they are very well adapted to grow and thrive in the fynbos region (Richardson et al., 2011). These invaders overcome the effect of low soil fertility by utilizing their synergism with *Rhizobium* spp. to fix atmospheric N, and have been shown to be more productive and hence more profligate users of

other resources such as water in the fynbos biome (e.g. Dye et al., 2004; Richardson and Rejmánek, 2011; Morris et al., 2011). The impact of the invasive woody species on soil processes are only recently receiving attention, however, none of these studies have so far looked at soil respiration and its role in C dynamics on the Mediterranean ecosystem per se, or, indeed the impact of invasive plants on these processes. Major efforts are underway to clear alien invasive trees and shrubs from natural (and modified) environments, and there is an expectation that the systems will return to their original state, though this has never been tested. Soil respiration can act as a good indicator of soil ecosystem function (Oyonarte et al., 2012), but has never been applied in this way to test function of cleared ecosystems compared to native and invaded environments.

One of the area most heavily invaded in the Cape Mediterranean environment are riparian ecotones (Dye et al., 2004; Le Maitre et al., 2011). Studies suggest invasive *Acacia* individuals are more productive and grow taller in riparian ecotones compared to native species; where they occur and management intervention has not been applied, invasive *Acacias* tend to establish and regenerate quickly to form dense, sometimes monoculture stands, entirely displacing native species (Holmes 2007; Richardson et al., 2007). Litter produced by *Acacia* species tend to have low C/N ratios, and thus one would expect their decomposition to proceed rapidly, releasing C, N and other nutrients quickly into the soil compared to native species, which tend to be sclerophyllous (Le Maitre et al., 2011; Naude 2012). Root density of these invasive plants tend also to be higher than native plants (Morris et al., 2011), especially where dense stands of invasive trees have established in riparian zones, soils of which tend to be sandy and porous.

Soil respiration in fynbos riparian ecosystem can be characterized by its magnitude and its temporal and spatial variability. The rate of soil respiration is controlled primarily by the rate of CO_2 production by biota within the soil, but is modified by factors influencing the CO_2 movement from soil to the atmosphere (Tufekcioglu et al., 2001). Generally, soil temperature (TS) and soil water content (GSWC) are considered the most influential environmental factors controlling R_S. Most important are fine root mass which present a more important control than soil organic matter (SOM) in soil CO_2 flux (Oyonarte et al., 2012). These factors interact to affect the productivity of terrestrial ecosystems and the decomposition rates of SOM, thereby driving the temporal variation of soil respiration (Wiseman and Seiler, 2004). Data from the mid-latitudes of the northern hemisphere have shown that soil respiration increases exponentially with increasing soil temperature (Lloyd and Taylor, 1994). Root respiration increases exponentially

with temperature in its low range when the respiration rate is limited, mostly by the TCA cycle (Coleman et al., 2004; Mills and Fey, 2004). Increases in soil temperature lead to greater rates of R_S until high values retard microbial function; this is the same pattern that is seen with soil moisture levels. Experimental studies overwhelmingly indicate increased soil organic C decomposition at higher temperatures, resulting in increased CO_2 emissions from soils (Coleman et al., 2004). Soil respiration varies seasonally and even during each day, due to changing in soil moisture and soil temperature. In addition, R_S is affected by the texture and quality of the soil, vegetation and biome type, the topography and the locations. Study on how diffusion based R_S in different soil types, under different conditions, store and released carbon might help to understand how C might change in the future.

In the MTE's ecosystems, soil water content (GSWC) is a major driver of ecosystem CO_2 efflux during periods of drought stress (Inglima et al., 2009). It is likely that this is influenced by increasing temperatures. Soil respiration is generally low in dry conditions (prevalent during later summer in MTE's) and increases to a maximum at intermediate moisture levels until it begins to decrease when moisture content excludes oxygen (O_2) (Saiz et al., 2006). This allows anaerobic conditions to prevail and depress aerobic microbial activity, for instance during and after winter rainstorms in MTE's, though these conditions are very ephemeral. Studies have shown that soil moisture only limits respiration at the lowest and highest conditions with a large plateau existing at intermediate GSWC levels for most ecosystems (Conant et al., 2004). Dry conditions may cause the cell membrane to lyse, or break, spilling the cell contents into the soil (Vargas and Allen, 2008).

Soil C cycling is impacted by plant traits which in turn affect both input and outputs (Mantlana 2008). One broad functional feature with strong implications for soil C is plant relative growth rates. Root respiration increase with increasing in GSWC, especially in dry ecosystems, however, root respiration response to soil moisture of individual species vary widely from species to species depending on life history traits. High levels of soil moisture depressed root respiration with the exception of wetland plants, which have developed specific mechanisms for root aeration (Coleman et al., 2004; Curiel-Yuste et al., 2004). Soil moisture is a key process also because it predicts organics matter decomposition and soil CO_2 efflux (Reichstein et al., 2002; Tang and Baldocchi, 2005). For example, fast growing species produce large inputs of readily decomposable plant material, while slow growing species typically allocate more C to defence and structural tissues, and produce smaller inputs of longer-lasting, nutrient-poor litter (Burton et al., 2004; Raich and Tufekcioglu, 2000). The quality of root and litter has a similar

strong effect on decomposition rates and root and leaf litter quality are largely independent (Evrendilek et al., 2008; Silver and Miya, 2001; Chapin et al 2003). Exotic *Acacia* spp. are known to possess high quality litter, which may decompose fast, and in this way increase microbial R_S, and also have faster growth rates compared to native fynbos riparian plants, which will increase root respiration (Morris et al., 2011).

The contribution of MTE's ecosystems to the global C cycle has received little attention in the past (Rey et al., 2002). This region has shown large climate shifts in the past because of global climatic changes (Luterbacher et al., 2006), and it has been recognized as one of the most prominent hotspots in future climate change projections (Giorgi and Lionello, 2008). Interannual variability is projected to mostly increase especially in summer season, which, along with the mean warming, would lead to a greater occurrence of extremely high temperature events which may affect R_S. This makes the MTE's a potentially vulnerable region to climatic changes as induced, for example, by increasing concentrations of greenhouse gases (Ulbrich et al., 2006; Lionello et al., 2006a). In addition, IAPs have been reported to change soils biogeochemical and soil physical processes (Yelenik et al., 2004; Vitousek et al., 1997) and thus R_S rates in invaded terrestrial ecosystems in MTE's regions (Marchante et al., 2007). Therefore, it is important to understand which environmental factors control R_S and how these factors affect CO_2 flux from soil, especially in areas with prominent wet and dry season where R_S is one of the main processes of C loss in the ecosystem (Conant et al., 2000). Despite the fact that fynbos biome is very limited geographically, it contains a high biodiversity of plants that are adapted to the stressful and dry conditions of long, hot summers with little rain (Sidney et al., 2007). Though little is known about fynbos riparian ecosystems that make up only a small proportion of the land surface**,** because of their prominent location within the landscape and the intricate linkage between terrestrial and aquatic ecosystems, and their contribution to global C sequestration should not be under estimated (Holmes et al., 2005). The importance and significance of ecosystem respiration may be better assessed in the riparian ecotones between transects of lowlands and adjacent uplands to provide a way to investigate the importance of vegetation mediating surface CO_2 efflux and IAPs because climatic and edaphic-conditions are largely similar across transects (Raich and Tufekcioglu, 2000).

Soil respiration and invasive plants impacts on R_S have been studied in different parts of the world, but there has not been much work carried out in South Africa (but see Zepp et al., 1996; Mills et al., 2005; Nyaga 2009; Makhado et al., 2011). Similarly, there are no studies carried out on soil respiration in the fynbos riparian ecotones. Soil respiration is a sensitive indicator of

ecosystem status and is therefore, a sensitive indicator of several essential ecosystem processes, including metabolic activity on soil, and conversion of soil organic C to the atmospheric CO_2 (Tufekcioglu et al., 2010). Soil respiration is also a good indicator of soil quality and soil fertility (Parkin et al., 1996). Because of this, R_S may shed some light on trajectories of restoration of ecosystem processes after removal of alien invasive *Acacia* spp. and the landscape perspective may also shed light on spatial variation in R_S in the fynbos biome.

We aim to compare seasonal variation of R_S in natural riparian, *Acacia*-invaded riparian, and in cleared riparian ecotones and to identify the environmental variables most likely to cause differences in R_S with the aim of gaining a better understanding of the impact of alien invasive plants and biophysical controls on R_S at different landscape positions, and to characterize the relative effect of IAPs on seasonal patterns of R_S. We compared R_S rates under natural, invaded, and cleared riparian ecotones. We expected that differences would emerge depending on invasive status and landscape position. We also examined the influence of environmental variables, litter mass, soil properties and root mass on soil CO_2 production in three distinct landscape positions over seven seasons. To our knowledge, this was the first study that compared R_S in riparian ecosystems within the three categories on invasion in the fynbos biome.

2.3 METHODS

2.3.1 Study species

The selected study species is *Acacia mearnsii,* which is a fast growing leguminous (nitrogen fixing) tree, native to Australia. In its invaded range, it threatens native habitats by competing with indigenous vegetation, replacing grass communities, reducing native biodiversity and increasing water loss from riparian zones (Richardson et al., 2007; Holmes et al., 2008). For example, *Acacia* species in creased nitrogen rates of the soil in Brazil (Nouvellon et al., 2012) and have a negative impact on major biome of the world as seen in South Africa (Yelenik et al., 2004; Crous 2010), costal dune of Portugal (Marchante et al., 2008) as well as to influence input of C/N, and microbial processes in Hawaii island (Allison et al., 2006) and California (Caldwell 2006), and increase CO_2 in the environment (Dukes and Mooney, 1999). *Acacia mearnsii* may reach 6-20 m in height (De Wit et al., 2001; Crookes and van Wilgen, 2001; Crooks 2002; Van Wilgen et al., 1998; Henderson 1995). The species is usually found in disturbed, mesic habitats at an altitude of between 600-1700 m. In its native range, *Acacia mearnsii* grows in a range of climates, including warm temperate dry climates and moist tropical climates. *Acacia mearnsii* is

reported to tolerate an annual precipitation of between 6.6-22.8 dm, an annual mean temperature of 14.7-27.8 °C, and a pH of 5.0-7.2 (Dukes and Mooney, 1999).

2.3.2 Site description

To investigate the effects of invasive alien plants *Acacia* species on fynbos riparian structure and function, we compared seasonal variability of soil respiration and selected biogeochemical processes in natural, invaded, and cleared riparian sites, at different landscape positions (altitude above the active channel).

All field experiments were conducted during March 2010 to October 2012 within the south-western Cape. The study areas were located on private farms and conservation areas of the south-western Cape, South Africa. The study sites were located between 15 to 80 km distances away from each other depending on the treatment and sites location. The area falls within the fynbos biome which is characterized by winter rainfall and summer drought, with more than 60 % of rain falling between 1000 and 2000 mm of rain per year, although in some areas (e.g., in the Jonkershoek Mountains) it might exceed 3000 mm (Sieben 2002). Six river systems within this province were selected for their variety of reach types, history of both alien invasive and clearing plants, and their relative close proximity to the research facilities and were divided into three treatments. Pristine or natural, *Acacia*-invaded and *Acacia*-cleared riparian ecotones and associated non riparian upland fynbos were established along the same channels. Two factors were taken into consideration when setting up the sampling plots, namely lateral (wet and dry banks) and the longitudinal upland or associated upland fynbos (Figure 1.1). Within each transect, four to five plots were located and all vegetation surveys were taken per quadrant ($1m^2$). The sites were, Eerste River at Jonkershoek (33°57'13.6" S; 18°58 '43.8" E), Dwars River in the Dwarsberg Mountains some 1320 m above the sea level at Kylemore (33°57'16.04"S; 18°58'47.78" E), Sir Lowry's Pass River at Sir Lowry's village in the Wedderville Estate (34°05'41.5" S; 18°56'39.7" E), Jakkals River at Bot River (33°12'31.81" S; 19°10'38.75" E), Molenaars River at Du Toits Kloof Mountains and runs through the town of Rawsonville (33°42'38.56" S; 19°11'49.24" E), and Wit River at Bainskloof (33°32'18.5" S; 19° 0'55.6" E) (Figure 2.1). There were four study areas (downstream and upstream) in Eerste River (33°59'22.28" S; 18°58'03.17" E), Dwars River (33° 56'5336"S; 19 58'11.25" E), Molenaars River (33°42'16.95" S; 19°13'59.42" E), and in Jakkals River (33°13'01.10" S; 19°12'25.84" E).

Site selection was based on the following criteria: natural riparian ecotones where the vegetation comprises predominately indigenous fynbos and riparian trees (the natural sites), *A.*

mearnsii at minimum 70 % canopy cover, or a mixture of *A. mearnsii* and other acacias (the invaded sites) and sites that has been cleared of *A. mearnsii* more than 7 years prior to commencement of the research (cleared sites). We summarized the river geomorphological characteristics in Table 2.1. Thus, we selected eleven study areas in total.

At the natural sites dominant vegetation was by fynbos plants and riparian trees. The most prominent families are *Metrosideros angustifolium*, *Brabejum stellatifolium*, *Brakelina*, *Ericaceae, Proteaceae, Iridaceae, Rutaceae* and *Aizoaceae* Graminoids, Annual Herb, perennial Herb, shrub, and some Geophytes. A number of the typical fynbos genera *Aspalanthus, Agathosma, Crassula, Erica* and *Pelargonium* are found in the area (Boshoff et al., 2000). These trees grew in the riparian areas closest to the river systems while the stands of fynbos are located furthest apart from the river in the upland areas.

The invaded site of Wit River site is located in the foothill of the sections of the river where the channel is very wide. The bedrock is deep in many places with stone bottom pools that are scattered over riffle/run sections (Brown and Sax, 2004). The geology of this channel system consists mainly of the Peninsula formation supporting Hawequas Sandstone Fynbos vegetation type (Rebelo et al., 2006). The site is located on private land and efforts have been made by the owner to clean up areas along the river, but many strips of heavily invaded *A. mearnsii* trees are still evident. On the southern side of the river, where our site is located, both the wet and dry bank lateral zone is heavily invaded by closed-stands of *Acacia. mearnsii* trees. Only a few scattered individuals of *A. longifolia* were evident under *A. mearnsii* canopies. The lower wet bank, however, does support Palmiet (*Prionium serratum*) and includes *B. stellatifolium*, *M. angustifolia* and *Morella serrate* with invasion being more prominent in the dry bank zone. Overall, most natural sites have near pristine native vegetation and all pristine plants were also found somehow in invaded and cleared sites except *Acacia* spp. that are prominent in invaded sites or sprouting bunches where cleared. There was a mixture of species diversity at invaded sites, and the vegetation consists of indigenous fynbos in the uplands areas and *Acacia* communities within riparian zones. At some invaded sites, species such as *Metrosideros angustifolium*, *Brabejum stellatifolium*, *Brakelina*, Graminoid, Annual Herb, perennial Herb, shrubs, Geophytes were found among natural riparian ecotones. Sandstone geology, while at DuToitskloof sandstone is mixed with igneous rocks. Invaded sites located in Bainskloof Wit River, Lower Jakkals downstream at Beaumont Wine Farm, and Lower Molenaars River at DuToitskloof (Figures 2.A and B). The Bainskloof site is situated in the Mountain Stream Transitional zone, while the three other sites (Dwars, Jakkals and Molenaars) are in the lower

Foothills, which has a lower gradient (Table 1.1). All sites were located alongside rivers and species composition was characterized by some similarity (riparian zones) with differences in plants species between sites occurred in the uplands areas. Cleared sites had most of its vegetation being restored with native species but since clearing of IAPs have increased land cover at the expense of grasses in some areas aboveground floor was covered with bunch of exotic grasses but indigenous plants such those find cited in natural sites were present if any, left during Working for Water and landowner clearing operations. However *Acacia* spp. were dominant in invaded sites and site structure was dense in *Acacia* stands sites than the rest ecosystems.

2.3.3 Soil respiration measurements

Commencing at least twenty-four hours before the first R_S measurements were taken, 15 PVC soil collars with an internal diameter of 10 cm and a length of 5cm were installed in the riparian and upland transects leaving a 1cm rim extending above the soil surface. Collars were used to avoid disturbing the soil within the soil chamber each time a measurement was being made. Where collars got disturbed or lost, these were replaced at least twenty-four hours before R_S measurements commenced. Soil respiration was measured using a LI-8100 portable C dioxide infrared gas analyzer (IRGA, Li-Cor Inc., Lincoln, Biosciences, USA), that had an 8100-101 soil chamber attachment. This is an automated system (Li-Cor Lincoln, NE) made of a hydraulic 10 cm survey soil chamber controlled by an electronic system, and IRGA measuring CO_2 densities. An auxiliary sensor interface allows the additional temperature or moisture sensors. The desired number and time of measurements was selected with a laptop computer connected to the IRGA. Soil CO_2 efflux was measured twice per day by placing a 10.7 cm chamber on the collars and measuring the rate of increase of CO_2 concentration over 2 min periods with a portable infrared gas analyzer connected to a laptop. Measurements were generally taken at mid-morning and mid-afternoon, once a season for two weeks in total: 15 (collars) x 11 (sites). Sample locations were of three types: the upland sites, with no riverine influence, the dry bank (inundated several times during the wet season, but mostly dry at the soil surface) and the wet bank, closest to the bank, and wet throughout. Every time a collar was sampled, two replicate R_S measurements were also taken at that collar. Depending on access to the site or other constraints, e.g. access and riparian topography, soil CO_2 efflux measurements were generally made between 09 h 00 and 17 h 00. Any plants growing inside the collars were regularly clipped at the ground surface to prevent any new root growth and influence on soil CO_2 effluxes. The soil collars and the soil chamber were opaque, so no photosynthesis was expected during R_S

measurements. We measured R_S rates as CO_2 flux µmol m^{-2} s^{-1}. Plots were established along three geomorphological zones (wet bank, dry bank, and upland fynbos, all within 120 m of each). Fire had passed through the area (Jonkershoek and Dwars River) in March 2009, but the regeneration of trees and grass vegetation was already taking place at the time of 2010 R_S campaign.

2.3.4 Soil temperature and soil moisture measurements

Along each transect (wet, dry, and upland area), environmental measurements were collected parallel to R_S measurements on every day of data collection from autumn 2010 to spring 2011. While measuring R_S rates, we simultaneously recorded soil temperature (°C) at 5 cm depth and volumetric soil moisture within the 12-20 cm depth (GSWC, %). Samples were placed into zip lock bags, labelled and transported to the laboratory. On arrival, samples were stored in the cold room at 4 °C for analysis. With each CO_2 efflux measurements, soil temperature was recorded using an incorporated soil temperature probe placed near the collar at 5 cm depth. Similarly, a soil moisture probe (Hydrosense, Campbell Scientific Inc., Australia) was used to measure volumetric soil water content of up 12 and 20 cm with each flux measurement. During the seven intensive sampling campaigns, soil samples using a metallic soil core were collected in the 5cm depth for gravimetric determination of water content, in addition to volumetric soil moisture described above. Initial mass of soil samples was collected in the laboratory with digital scale and samples were dried in an oven at 105 °C in the laboratory for measuring dry mass on the same scale.

2.3.5 Supplementary soil information

Soil bulk density was determined in spring 2010 and autumn 2011 by taking soil cores of known volume at 5cm depth. We used a hand held standard core steel sampler (4.5 cm internal diameter and 25 cm height) to collect soil samples. For each site, one soil core was taken within two meters from each soil collar (to avoid disturbance) making a total of 15 to 12 samples per site. Soil bulk density was determined on separate and unaltered core samples. The weight of water was determined as the difference between the weight of the sample and its weight after oven drying at 105 °C for twenty four hours. Bulked soils cores were separated and tested for soil texture, pH, and water holding capacity (WHC %).

In September 2010 we used the rapid method developed by Kettler et al. (2001) to examine soil physical proprieties, and to test for differences in soil particle size and distributions. This method

was followed as described by Kettler et al. (2001), except that clay and silt passed through sieved mesh (2 mm) in a 350 ml beakers and rinsed with 250 ml deionised water.

Aboveground litter mass was collected at each study site during the following seasons: spring (2010), autumn (2011), and spring (2011). Litter mass was collected by placing randomly a 25 cm^2 wooden frame, and then picked up all litter inside the frame. The collected litter was placed in a labelled litterbag and taken to the laboratory. However, no classification of litter (e.g. coarse, fine, etc.) was made. In the laboratory, litter collected were bench-dried for two to three days, then oven-dried at 70 °C for 24 hours until samples achieved a constant weight.

Ten soil cores 0-10 cm depth for determination of root mass were taken in 2010 and 2011 using a sequential soil cores method from Vogt and Persson (1991), modified by (Robertson et al., 1999). In total, 150 bulked soils were collected per site and samples placed in sealed plastic bags and kept in a cooler box immediately after collection and taken to the laboratory for further processing. In the laboratory, soil samples for root masses were processed, sieved through a 2 mm mesh and washed free of soil with distilled water (Vogt and Person, 1991), weighted and oven dried for 24 h at 60 °C until it reached its constant weight, then weighted the next day. No attempt was made to distinguish living and dead roots (Vogt and Persson, 1991; Benjamin and Nielsen, 2004).

2.4 DATA ANALYSIS

The effects of the three different riparian ecosystems (natural, invaded, and cleared) on R_S rates were compared to the treatment and landscape position and comparisons among means were made across seasons using the least significant difference (LSD) test calculated at $P < 0.05$ using analysis of variance (ANOVA) as provided in the program Statistica (StatSoft, Inc, version 10.0.). Invasion status, landscape position and season were fixed factors and grouped in sites with sites as random factor. Nevertheless, fixed factors were used as the main effects and differences between individual sites were not tested. When interacted with treatments and landscape positions (wet, dry banks and terrestrial areas) across seasons with seasonal variation within group were tested with repeated ANOVA and a post hoc test was applied when necessary. We used data from all 11 sites in the analysis although invasion is most established in riparian dry bank zones. But when tested across invasion status, one-way ANOVA was used to test the difference between treatment and landscape position. The effect of soil temperature,

soil water content, bulk density and root mass upon R_S was also tested using LSD test (StatSoft, Inc, version 10.0.228.2).

2.5 RESULTS

2.5.1 Soil respirations by invasion status and landscape position

Seasonal R_S rates measured within natural, invaded and cleared sites during the study seasons ranged from 2.55 (± 0.21) µmol CO_2 m^{-2} s^{-1} at natural sites, to 4.18 (± 0.18) µmol CO_2 m^{-2} s^{-1} in the *Acacia*-invaded, and 2.09 (± 0.21) CO_2 µmol CO_2 m^{-2} s^{-1} at cleared riparian sites (Figure 2.1). Over the course of the study, R_S was highest in dry season, the summer, and no significant differences were evident between R_S. During summer, the mean R_S rates were 4.15 µmol m^{-2} s^{-1}, and ranged from 2.05 µmol m^{-2} s^{-1} to 2.59 µmol m^{-2} s^{-1}. During autumn and winter (2011), R_S rates declined again, reaching values close to those in winter and autumn 2010 (Figure 2.1A and B).

Soil respiration is different between sites with different invasion statuses and landscape positions and large differences in soil CO_2 efflux were evident ($F_{[12, 74]} = 1.19$, $P = 0.28$) (Figure 2.1A and C). Soil respiration increased seasonally in both riparian zones and upland areas, with a summer peak of approximately 7.34 µmol m^{-2} s^{-1}. All riparian ecotones showed the same seasonal trends in their soil CO_2 efflux, however, there was a significant interaction of overall R_S rates in terms of treatments and landscape positions ($F_{[4, 16]} = 6.07$; $P = 0.003$; $P = 0.00$; Figure 2.1C). High CO_2 efflux rates were associated with dry banks and wet banks that are invaded. On average, invaded dry banks had the rates of 3.36 µmol m^{-2} s^{-1} dry banks and invaded wet banks of 3.05 µmol m^{-2} s^{-1}. This is compared to natural and cleared wet and dry banks which was approximately 0.8 to 1.50 µmol m^{-2} s^{-1} lower in the natural and cleared sited. There were no significant differences between wet and dry banks of the latter two invasion statuses. Also notable is that there were no significant differences between terrestrial areas of any invasion status; none of the sites had significant *Acacia* invasion.

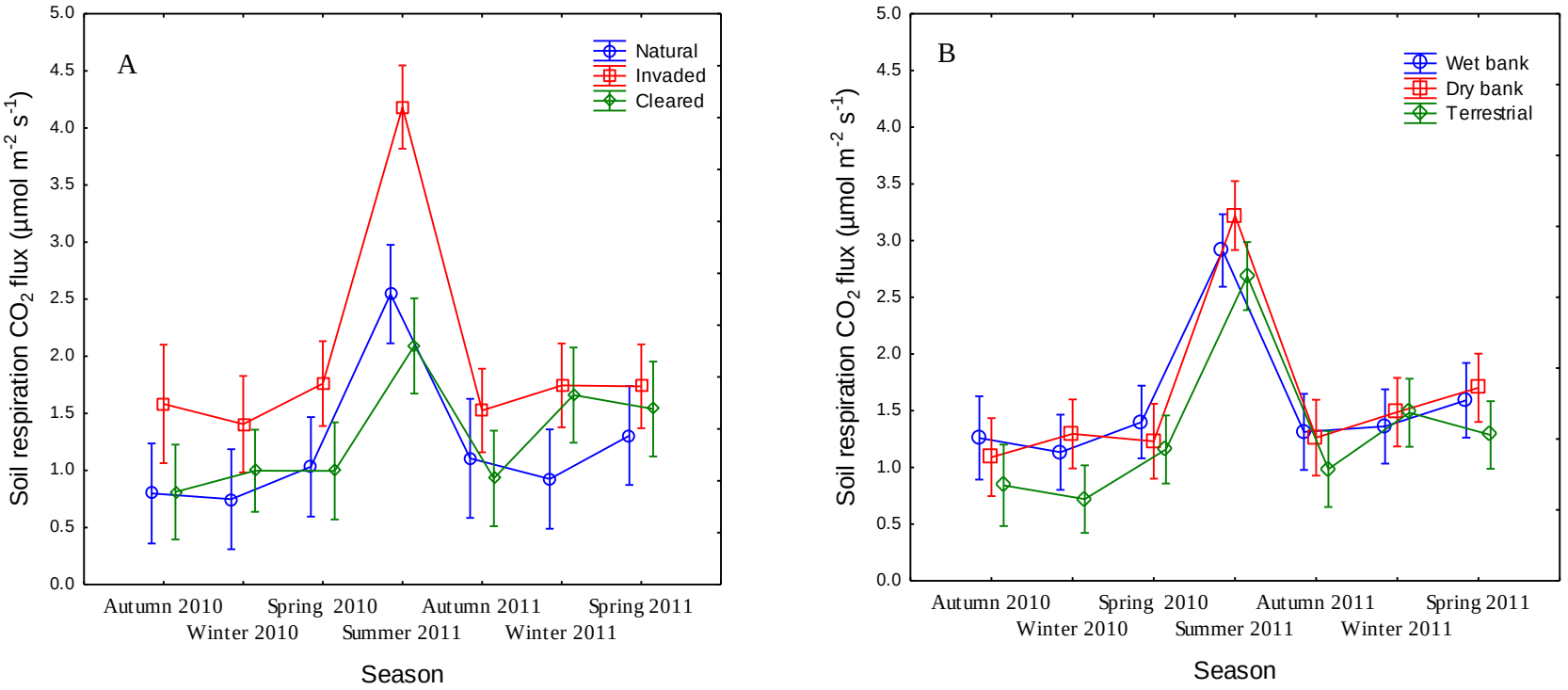

Figure 2.1: Soil respiration by landscape positions. Mean (±SE) seasonal soil respiration surface CO2 efflux within treatments and across seasons (A) and soil CO2 efflux across landscape position within seasons during seven campaigns (B), and (C) is the differences between soil respiration in natural, invaded, and cleared riparian sites (invasion status) across micro-sites (wet bank, dry banks and terrestrial areas or uplands) surface CO2 efflux at landscape position. Different letters denote significant difference at $p < 0.05$ analyzed using LSD test.

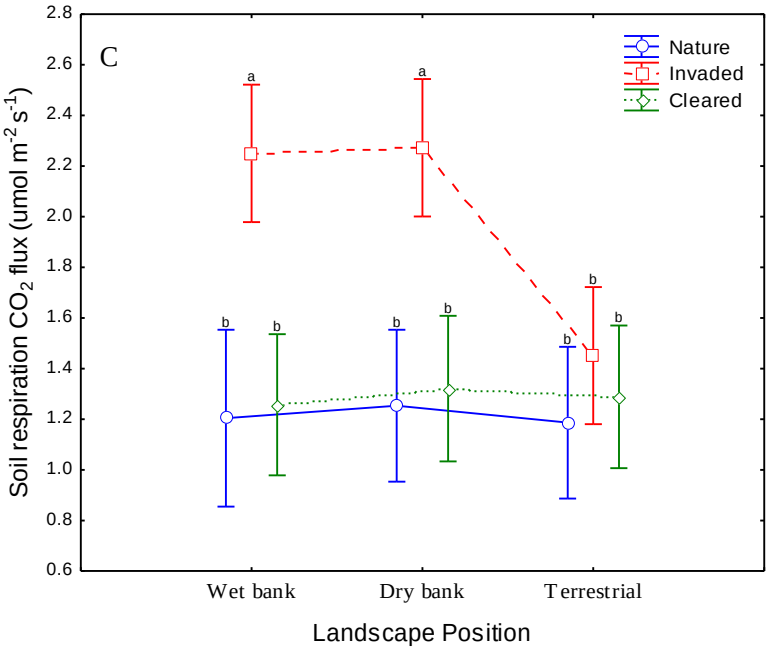

Figure 2.1: (Continued). Soil respiration by landscape positions.

2.5.2 Drivers regulating in situ soil respiration

Based upon all the data gathered during two years of seasonal field gathering (March 2010 and October 2011), there was no significant relationship between soil temperature across treatment and landscape positions. Both temperature and gravimetric soil water content (GSWC) contributions to total R_S changed significantly between seasons and landscape positions but was consistently higher in riparian zones (Figure 2.2B). Seasonal surface CO_2 efflux was lowest during the wet periods (winter), when soil temperature was lowest at all locations, but also wettest (Figure 2.2B, F = 36.38, df = 6, P = 0.00). Soil temperature varied between seasons and riparian statuses at landscape position (Figure 2.2A). Soil temperature was high during dry season and lower in wet and cold season (Table 2.1, $F_{[6, 38]} = 22.53$, $p < 0.05$). Maximum soil temperature (30 ºC) coincided with minimum GSWC (5 %) during the dry season campaigns whereas minimum CO_2 effluxes were measured during the same season (summer) (Figure 2.1A). Average soil temperature at both riparian zones and upland areas varied from 10.25 to 17.88 (± 0.92 °C) in winter, and about 25-30 ºC during summer campaign. The maximum soil temperature was recorded in summer (32.70 °C). Soil temperature slowly declined by ~ 5 °C in early autumn 2010 at most all sites (Figure. 2.2A). Slightly differences in soil temperature emerged in invaded and cleared sites when compared to natural, averaging 20.40 °C in invaded and 19.74 °C in the cleared sites across seasons. Soil temperature was significant different among seasons and was lowest in winter and highest in summer when CO_2 efflux increased to

its maximum $P < 0.05$. However, some differences in soil temperature were observed between treatments and landscape position (Table 2.1, means including all seasons).

Soil water content also varied among seasons, generally increasing in autumn and winter and decreasing in spring and summer ($F_{[2, 16]} = 27.87$, $P = 0.07$; Table 2.1). Soil temperature also showed the same trend during the winter period all over riparian statuses. Soil moisture was higher in natural than in cleared sites (13.37 %), and *Acacia*-invaded sites ($F_{[2, 9]} = 0.65$, $P = 0.54$). Mean soil water content was around 20.5 % in wet banks, 10.2 % for dry banks and 5.8 % in terrestrial areas (Figure 2.2B). Soil moisture was significantly different (Table 2.1) and was highest in natural site (wet banks) during the course of this study (show stats). There were significant differences between riparian zones and upland areas among treatments, with high soil moisture measured in wet banks (Figure 2.2B) ($F_{[24, 747]} = 2.87$; $P = 0.000$). Riparian soils were constantly drier during summer following the decline in rainfall as expected. This drop of soil water content during summer period was, however, more pronounced in dry banks and upland zones. The different in soil moisture between dry and upland areas were less apparent as dry banks were only different from upland areas much in winter.

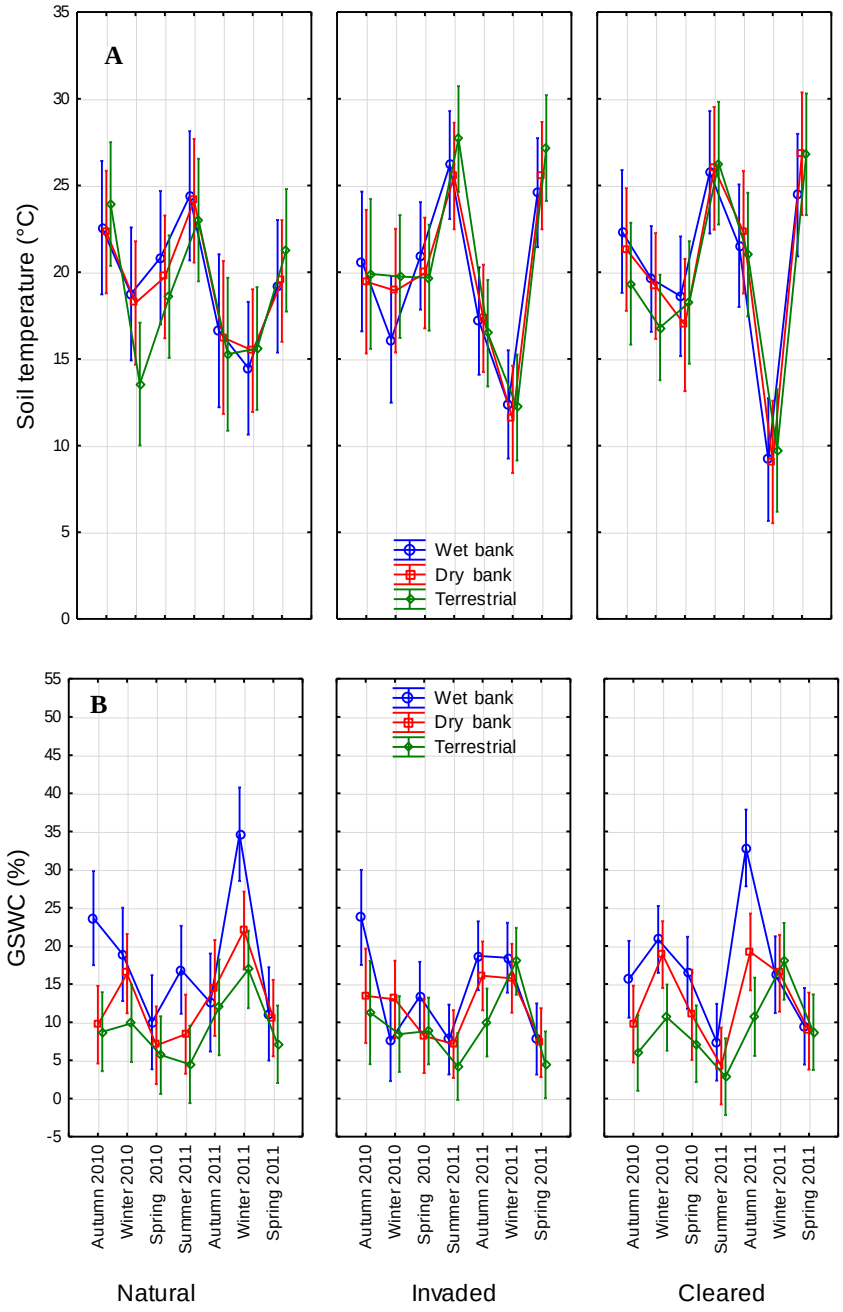

Figure 2.2: Measured mean soil temperature. Measured mean soil temperature (°C) at 0-5 cm depth (A) and gravimetric soil water content (%) at 0-5 cm and volumetric water content (0-12 and 0-20 cm) depth (B) in riparian ecosystems across seasons. Data are means and standard errors for 7 campaigns and are characterized by landscape and invasion status. Graph showing seasonally differences in soil temperature and soil water content within each sampling season. Blue color represents wet banks, red dry banks, and green colour upland areas.

Table 0.1: Analysis of variance (ANOVA) statistics. Analysis of variance (ANOVA) statistics for riparian zones and uplands transects versus treatment, seasons, soil temperature (TS, °C), gravimetric soil water content (%) and surface CO_2 efflux µmol m^{-2} s^{-1} (0-5 cm depth) from autumn 2010 to Spring 2011. (DF: Degrees of freedom, F: Statistics, P: Probability F value at P < 0.05.

	Source	DF	F	P-value	Significance
Invasion status X Landscape position	R_S	4	6.11	< 0.05	***
	TS	4	1.67	-	n.s
	GSWC	4	0.76	-	*
Invasion status X Season	R_S	12	3.87	-	***
	TS	12	1.85	-	n.s
	GSWC	12	3.51	-	***
Landscape position X Season	R_S	12	1.22	-	*
	TS	12	2.32	-	n.s
	GSWC	12	2.97	-	***
Invasion status X Landscape position X Season	R_S	24	1.25	-	*
	TS	24	1.54	-	***
	GSWC	24	2.60	-	***

n.s *indicates non significance,* ******* *: significant and ***: indicates highly significant at P < 0.05.*

Soil water content alone was a very poor predictor of surface CO_2 efflux in the MTE's, but when R_S and all variables data were viewed together, some trends emerged. The combined effect of soil temperature and soil water content on R_S accounted for a considerable amount of variation within invasion status, with R^2 values of 0.31 and below (Figure 2.3A). Notably R_S is positively related to both soil temperature and GSWC depending on the season of the year (Figure 2.3A-F). However, seasonal relationships between R_S, soil temperature, and GSWC were different, based on the shape of the curves, and the strength of the relationships. Soil respiration was correlated with soil temperature over all seasons within invasion status and was highest in

invaded sites (Figure 23.A-D; R^2 = 0.31. Soil respiration decrease with increase GSWC and was negatively related to soil water content over all sites (Figure 2.3B). Very prominent, nevertheless, is the ranges where maximum surface CO_2 efflux takes place. Soil CO_2 effluxes are highest at GSWC < 20 %, with maximum values between 0 and 5 %. This was apparent within landscape position. The strength of the relationship between soil temperature and R_S did not vary between landscape positions; for wet banks R^2 = 0.21, dry banks R^2 = 0.21, and for terrestrial areas R^2 = 0.22 (Figure 2.3C). Soil water content was positively correlated with R_S in invaded sites and negatively in natural and cleared sites (Figure 2.3D). However, on average soil temperature had a limiting overall effect on R_S over all seasons (R^2 = 0.29, $P < 0.05$), but GSWC showed an opposite effect on mean R_S (Figure 2.3E and F, R^2 = 0.30). There was seasonal variation in soil temperature and soil water content among invasion statuses each with its trends depending on the season of the year.

Mean R_S rates were typically lowest during the wet season in autumn and winter depending on the invasion statuses and was high during dry seasons. However, when breaking down the R_S and soil temperature and moisture relationships further more clear relationships emerged, with highest R_S recorded between 25-30 °C (Figure 2.3G). Some trends emerged, notably that R_S is positively related to soil temperature and negatively to GSWC or both during summer (Figure 2.3A1-G2). However, these relationships were dependent on riparian statuses and season of the year. However, seasonal variation in soil temperature, GSWC across landscape positions were also assessed (see Appendix Figure A1.1 and A1.2) During both years, the highest soil temperatures were measured in spring and summer (25 °C and 32 °C) coinciding with lowest soil water content values (~5 %). Soil temperature was significant different during the seasons of each year. In autumn 2010, the relationship between R_S and soil temperature was different with the low rates of R_S observed in March 2010.

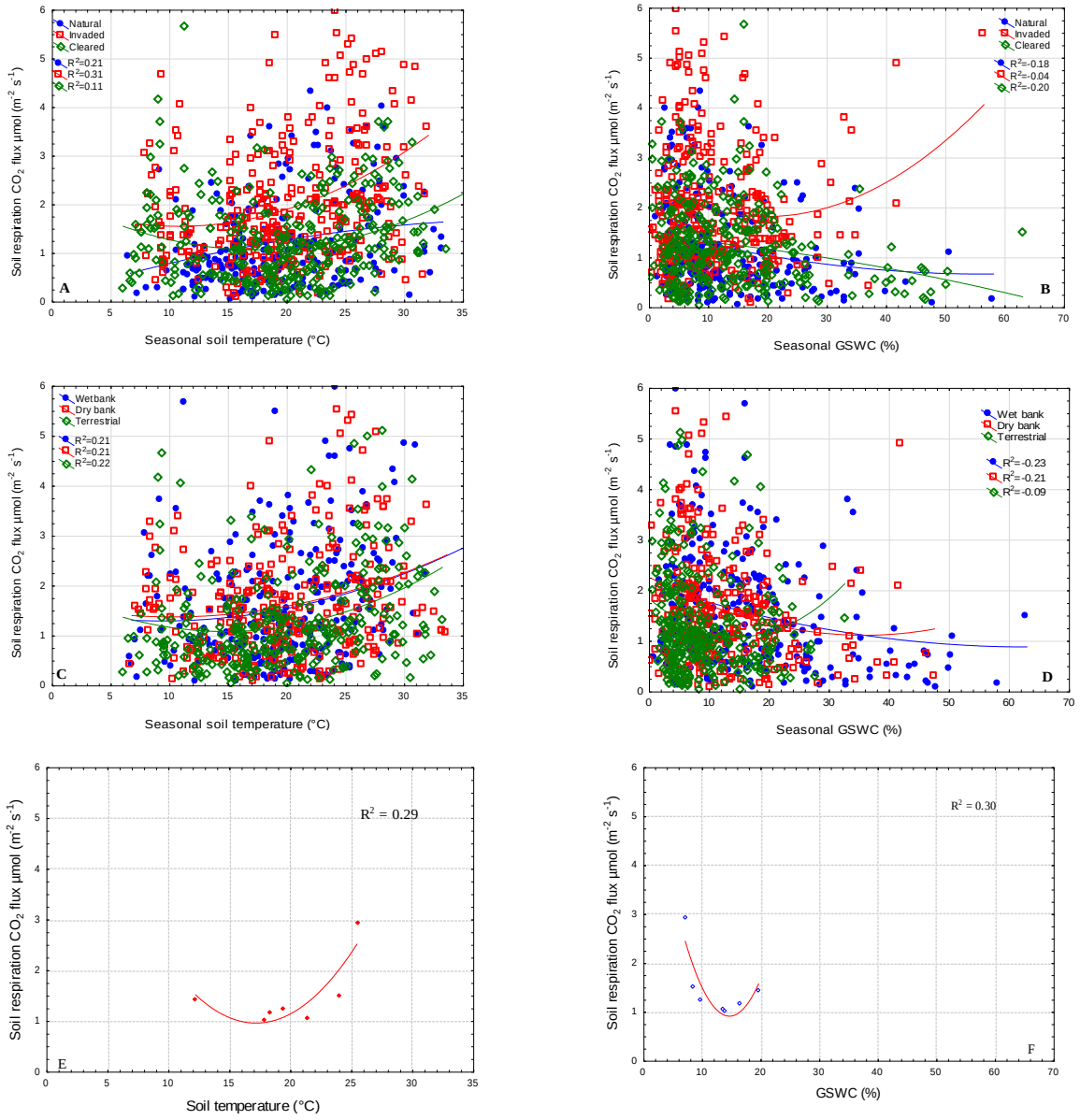

Figure 2.3: Seasonal relationship between soil respiration and soil temperature by treatments (A) and between seasonal soil respiration against gravimetric soil water content by invasion statuses (B), seasonal relationship between soil respiration and soil temperature by landscape positions (C) and interactions between soil respiration CO_2 effluxes and soil water content by landscape position (D). Above Figures represent the relationship between mean soil respiration rates against mean soil temperatures at 0-5 cm depth; soil respiration as function of soil temperature (E) and soil respiration against mean gravimetric soil water content at 0-5 cm depth (F) for seven consecutive seasons, from March 2010 to October 2011 and all relationship are fitted with polynomial curve.

The results concerning soil respiration as function of soil temperature and soil water content are presented in Figure 2.4. For each season and invasion status, soil respiration is represented for the three landscape positions. Figure 2.4A1-G2 shows relationships between soil respiration, soil temperature and GSWC with increasing soil CO_2 efflux as a function of either temperature or GSWC. In summer, soil respiration rates increased when soil temperature was 20-25 °C and decreased when soil temperature reached a maximum of 31 °C and was highest in invaded sites with no difference observed natural and cleared sites (Figure 2.4D1). A similar relationship was observed between R_S and GSWC during summer (Figure 2.4D2). Soil respiration increased with increasing GSWC in invaded sites (R^2 = 0.47); no such trends were observed in cleared and natural sites. Soil respiration in invaded sites seemed to be more temperature controlled and was highest when soil moisture was low (0-10 %) and decreased when sol temperature reached a maximum of 32 °C. In spring 2010, soil temperature of 12-20 °C increased soil CO_2 efflux in invaded sites (Figure 2.4C1; R^2 = 0.13) while it generally deceased in natural and cleared sites. However, above 20 °C, R_S declined in invaded sites in spring 2010. Generally in spring 2010, R_S declined with increasing GSWC, except for the invaded sites, which showed an increase with increased soil moisture, with an R^2 = 0.29 (Figure 2.4C2). A similar trend was also observed in winter 2010 with an R^2 = 0.36 for the relationship between R_S and GSWC, and very weak relations for the other invasion statuses, and similarly for soil temperature (Figure 2.4B1 and B2).

During the first and second autumn campaigns, relationships were generally weak, except for cleared sites in 2010, where soil CO_2 effluxes increased with an increase in soil temperature (R^2 = 0.50; Figure 2.4 A1). Though, autumn 2011 soil respiration increased with an increase in soil temperature in cleared sites (R^2 = 0.25) with weaker relationships in invaded and natural sites. Overall, the relationship between soil moisture and R_S was negative for the autumn seasons, regardless of invasion status (Figure 2.4A2 and E2).

In general, when all season and invasion statuses were categorized and arranged by riparian types, different curves were observed and were influential in different seasons (Figure 2.3C). Therefore, soil respiration responds differently to temperature and GSWC depending on season and invasion statuses of the sites. Typically, soil respiration was highest during the warm and drier periods (summer and spring) than in cold and cool seasons.

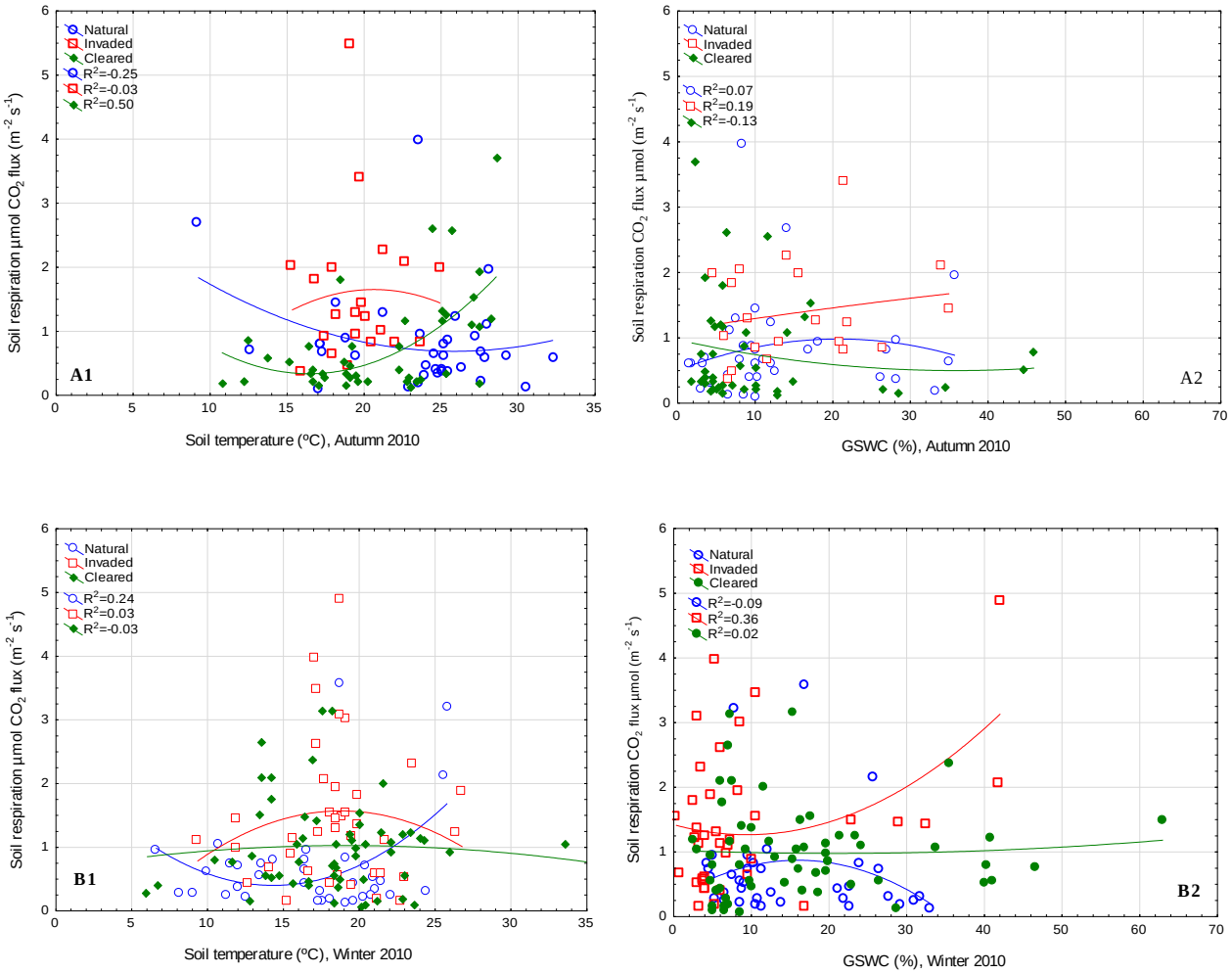

Figure 2.4: Mean soil respiration (µmol m^{-2} s^{-1}) plotted against mean soil temperature and gravimetric soil water content gathered by season and among invasion statuses from autumn 2010 to spring 2011. From left to the right panel is the relationship between R_S plotted against soil temperature and GSWC for autumn 2010 season (A1-A2), for winter 2010 (B1-B2), for spring (C1-C2), summer (D1-D2), autumn 2011 (E1-E2), winter 2011(F1-F2), and spring 2011 (G1-G2) as a regression function of soil respiration fitted with polynomial trendline or curve.

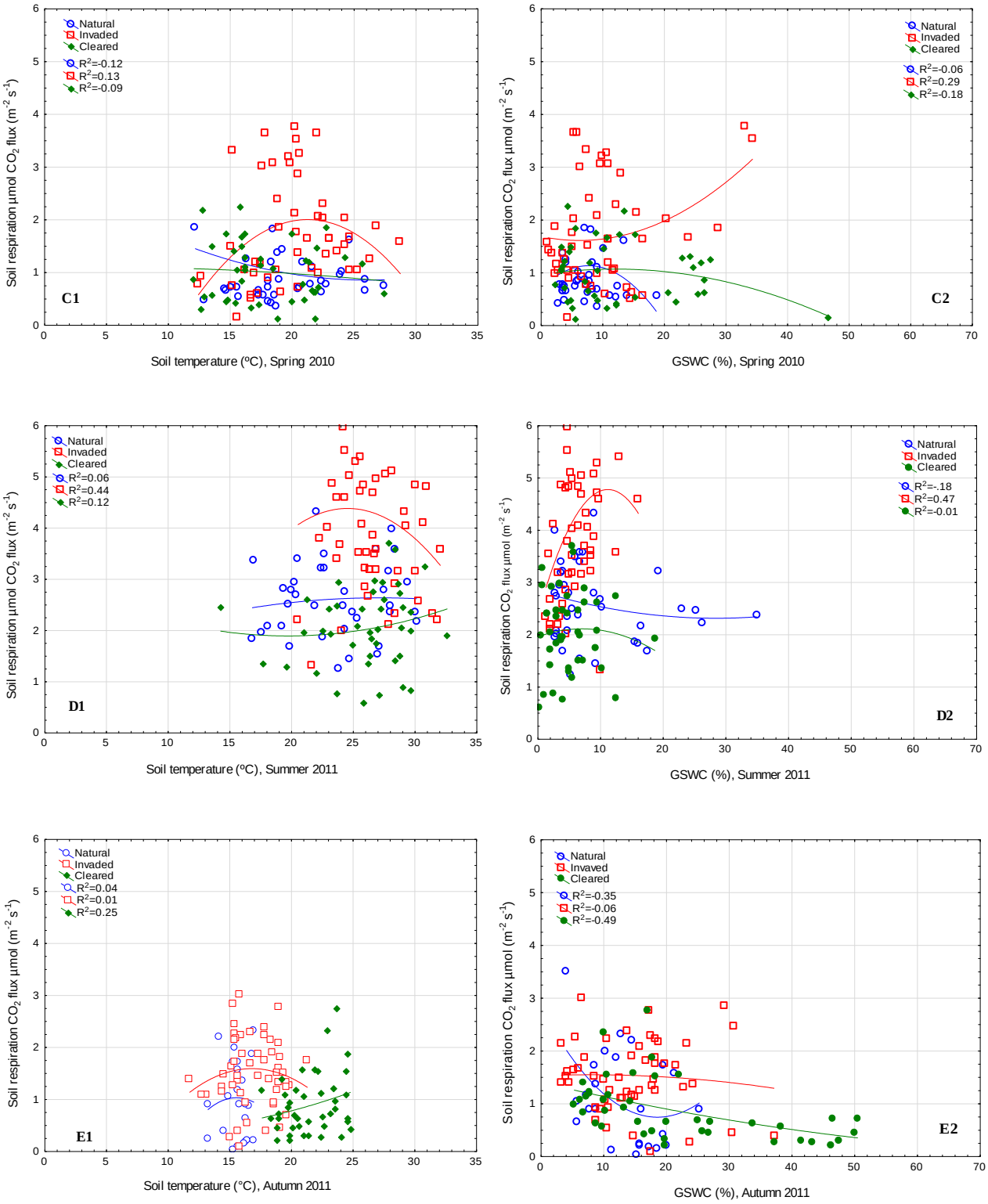

Figure 2.4 (Continued)

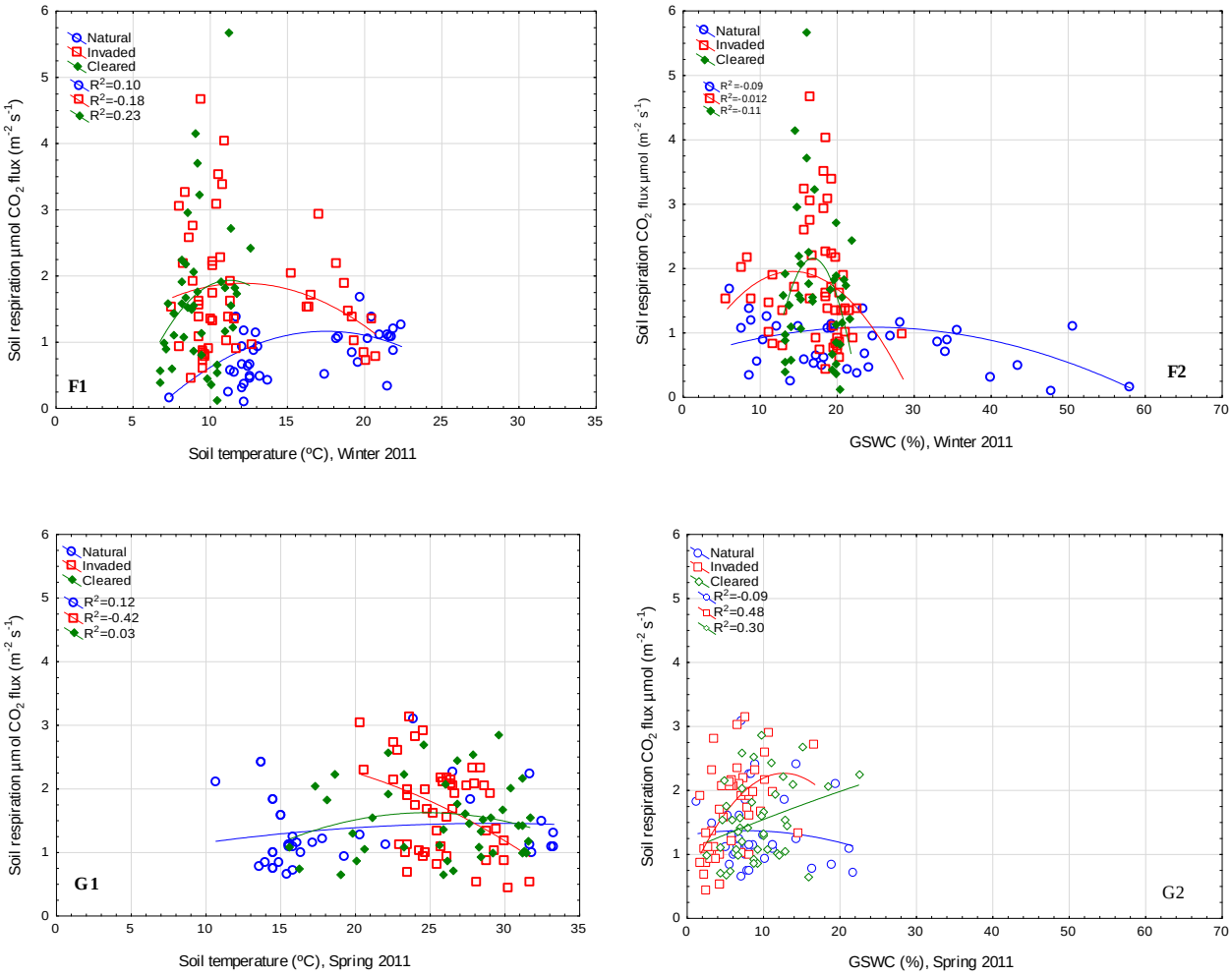

Figure 2.4 (Continued)

2.5.3 Soil characteristics and plant biomass

Our results showed that, there was significant differences in litter mass among seasons and invasion statuses (F = 3.12, P = 0.00). Over all, higher rates of litter biomass was found in autumn 2011 (Figure 2.5A) and was higher in *Acacia*-invaded sites and within riparian zones (Figures 2.5A and B). As expected, natural and cleared sites had lower litter mass and seasonal means litter mass were not statically different from each other. Seasonal aboveground litter mass was lower within invasion statuses in spring 2010 compared to litter mass collected in autumn 2011. During 2010, litter mass was slightly higher at invaded sites with mean values of 6.08 (± 1.39) kg, followed by natural sites with 4.36 (± 1.11) kg, and cleared sites with lowest litter mass of 2.58 (± 0.61) g m^{-2} observed at cleared sites but these differences were no statically significant (P = 0.05). Whereas, autumn 2011 seasonal litter mass from invaded and cleared sites was significant different with 6.06 (± 0.91) kg - 7.65 % measured in natural, 15.66

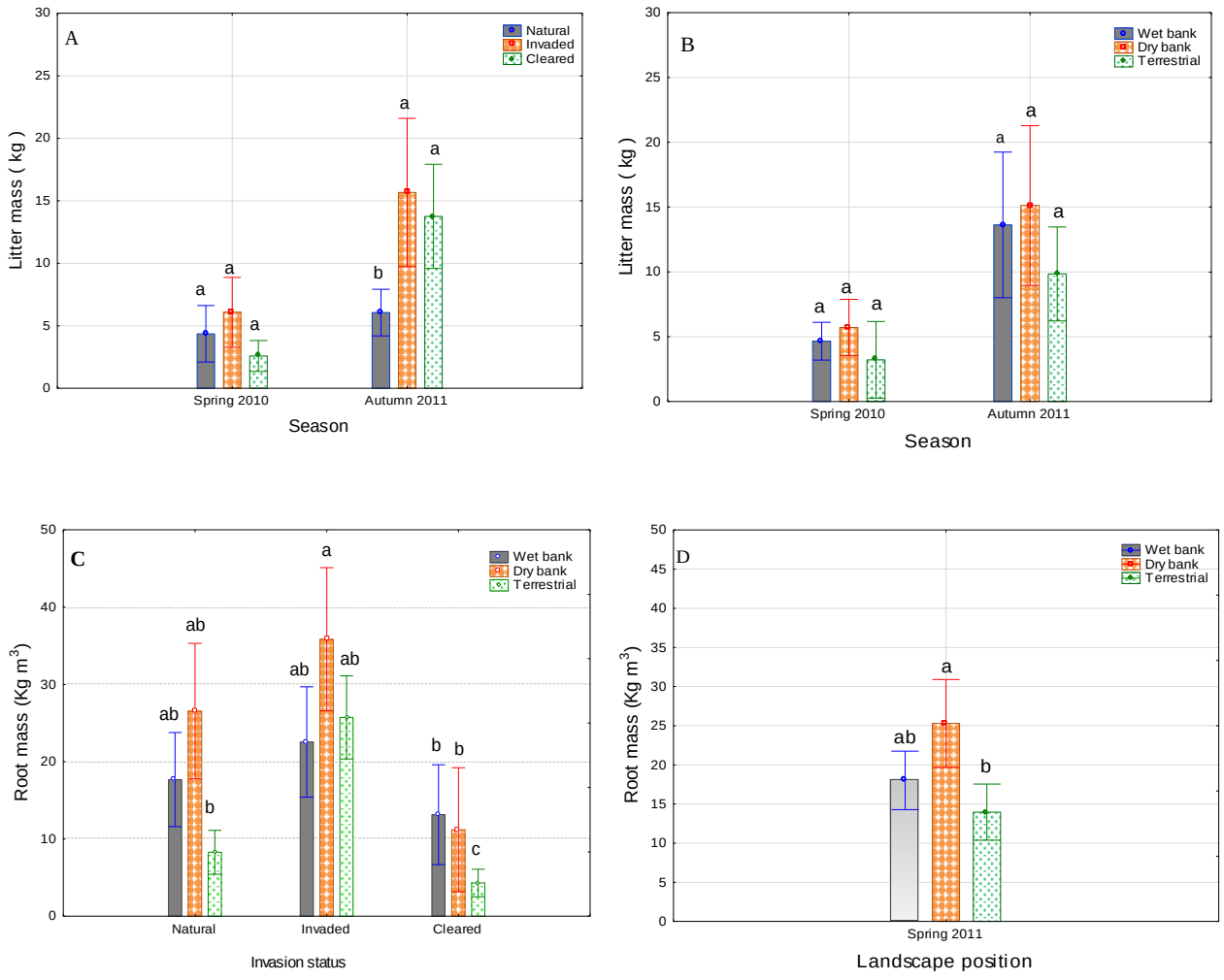

Figure 2.5: Seasonal mean litter mass collected during two seasons of different years spring 2010 and autumn 2011 by invasion status Seasonal mean litter mass collected during two seasons of different years spring 2010 and autumn 2011 by invasion status (A) and by landscape position (B). Root mass values collected during spring 2011 showing all data arranges by invasion status and landscape positions (C) and all data combines (D). Points are means and whiskers standard errors. Means with different letters are significantly different at $p < 0.05$ using an ANOVA followed by the LSD.

(± 2.94) kg ~37.5 % found in invaded sites, and 13.75 (± 2.06) with approximately 27 %. Litter mass was lowest during 2010 and ranged from 4.66 (± 0.71) g m^{-2} in wet banks, 5.72 (± 1.07) in

dry banks and 3.22 (± 1.47) in terrestrial while autumn 2011 was highest with wet banks having 13.62 (± 2.77), 15.12 (3.04) at dry banks, and 9.84 (± 1.79) at terrestrial areas. Overall, spring 2010 had 28 % litter mass compared to 72 % in autumn 2011. There was no difference in litter mass across landscape position during spring 2010. However, autumn 2011 was significantly different ($F_{[5, 247]} = 6.47$, $P = 0.001$) and was highest in wet and dry banks (Figure 2.5B). Dry banks had high rates of litter mass (20.26 (± 1.87) followed by wet banks (13.96 (± 2.01) and the terrestrial areas with 10.17 (± 1.85 (Figure 2.5A and B)) gm^{-2}. Spring 2010 had lowest litter mass within landscape position than that found in autumn 2011. Mean seasonal root mass rate was significantly different within *Acacia*-invaded sites (Figure 2.5C, $F_{[2, 7]} = 10.17$, $P = 0.00$).

As we expected, there was a significant variation in mean root mass between invasion statuses and within landscape position during spring 2011 ($F_{[8, 127]} = 10.79$, $P = 0.00$). Mean root mass was different between seasons and among treatments with higher root density measured in autumn 2011. We used a soil core cylinder sampler (10 cm tall with internal diameter of 4.5 cm) of known volume 159.04 g/cm^3 and convert into kg m^3. Average values of 21.83 (± 2.01) K gm^3 was measured in invaded, 14.38 (± 2.41) Kg m^3 in natural sites and 8.17 (± 2.28) Kg m^3 measured in the cleared sites (Figure 2.5C). Overall, root density showed similar trends as previously seen with litter mass. There was no difference in root density between riparian statuses in spring 2010 than found in autumn 2011 with invaded sites showing the highest root density. Lowest rate of root density was found in cleared sites and within the terrestrial areas of the landscape position (Figure 2.5D).

We used Spearman's correlation coefficients to determine relationships with other soil chemical and physical properties and also with cover of various functional types of vegetation. The strongest relationships that emerged was between invasive cover, with adult *Acacia* trees showing a correlation of 0.60 and seedlings *Acacia* a correlation of 0.52 with CO_2 emission during autumn 2010 (Table 2.3). Soil particle size, particularly silt and clay also was significantly correlated with R_S, showing a coefficient of 0.61. None of the other factors tests showed correlation coefficients higher than 0.25 (Table 2.3).

Table 0.2: Correlation coefficients testing the effect of plant biomass and selected physical-chemical properties of soil in different seasons and their interactions on soil respiration rates Correlation coefficients which tested the effect of plant biomass and selected physical-chemical properties of soil in different seasons and their interactions on soil respiration rates between invasion statuses and across landscape position in riparian and adjacent fynbos during that particular season.

	Sources	**R_S µmol (m^{-2} s^{-1})**		
Season	Plant & soil	CO_2 efflux	n	*P*-values
Autumn 2010	IAPs (seedling)	0.60***	32	0.001
Autumn 2010	IAPs (young trees)	0.52***	32	0.02
Autumn 2010	IAPs adult (> 2m) CC	-0.41**	32	0.18
Autumn 2011	Litter mass (g)	0.14*	120	0.05
Spring 2010	Medium to fine sand	0.21*	138	0.05
Spring 2010	Coarse sand	-0.23**	138	0.10
Spring 2011	Root density (g m^{-2})	0.14*	132	0.05
Summer 2011	Soil pH (water)	-0.15**	87	0.12
Summer 2011	slit & clay (<0.053 mm)	0.61***	137	0.001

Total n = 848; *P < 0.05; **P < 0.1 ***P < 0.001

Table 0.3: Summary of soil respiration rates reported for other biomes compared with those measured in Mediterranean region of the south-western Cape measured in this study. Values represent mean ± standard deviation where available.

Ecosystems	Soil respiration rates µmol CO_2 efflux (m^{-2} s^{-1})	Sources
Semi-arid savanna ecosystem (Kruger National Park, South Africa)		Makhado and Scholes, 2011
Acacia	1.053	
Combretum savannas	0.831	
Subalpine (Montana, United states of America)		Pacific et al., 2009
Wet season 2005	0.5-1.00	
Dry season 2006	0.5-1.00	
Harvard Forest (USA)		Phillips et al., 2010
Upland	2.94	
-	4.51	
-	4.78	
-	4.86	
-	5.73	
Wetland	3.06	
-	3.80	
-	3.89	
-	3.42	
-	4.25	
Savanna, (Okavango Delta, Botswana)	0.3	Mantlana 2008
Rain-fed grassland	8.8	
Seasonal floodplain	2.7	
Intermediate food		

Ecosystems	Soil respiration rates µmol CO_2 efflux (m^{-2} s^{-1})	Sources
Mediterranean (California, USA)		Ma et al., 2005
Ceanothus-dominated patches	2.0-4.5	
Open Canopy	0.9-2.9	
Post Oak Savanna, Texas (USA)		Thompson 2011
Grass untreated	2.99	
Grass heated	2.57	
Grass unheated redistributed precipitation	2.53	
Grass heated redistributed precipitation Juniper untreated	2.51	
Juniper heated	2.93	
Juniper untreated	3.39	
Juniper untreated redistributed precipitation	3.08	
Arid Ecosystem (representative ecosystems of the Natural Park, south Spain)	2.97	Oyonarte et al., 2012
Dry period(summer)	0.40	
Growing season (spring)	1.93	
Shrublands	0.25-0.89	
Agriculture soils	1.70-2.00	
Bare soils	0.43-1.85	
Tropical rainforest (Rio Branco, Brazil)		Salimon et al., 2004
Wet and Dry seasons (year round)	7.26 ± 0.13, 6.94 ± 0.06, and 6.00 ± 0.13	
Mediterranean fynbos biome (South Africa)		This study
Natural riparian	0.31 - 2.89	

Ecosystems	Soil respiration rates µmol CO_2 efflux (m^{-2} s^{-1})	Sources
Acacia-invaded riparian	0.47 - 5.65	
Acacia-cleared riparian	0.22 - 2.53	
Riparian zones (wet banks)	2.91	
Riparian zones (Dry banks)	3.22	
Upland fynbos (Terrestrial)	1.16	

2.6 DISCUSSION

Mean R_S values found in our study are not dissimilar to the few data available for Mediterranean and other ecosystems with pronounced dry seasons. Average summer CO_2 efflux of approximately 5.65 µmol m^{-2} s^{-1} and appear to be closer to that previously reported in Mediterranean climate region of North America (California) by Ma et al. (2005) and in central Montana (Pacific et al., 2009). Our results agree with the lower R_S rates reported in central Queensland region (Kaur et al., 2006) between cleared and uncleared native *Eucalyptus populnea*, *E*. *Melanophloia* and *Acacia harpophylla* and was similar to R_S rates under agricultural field (pear, apple and citrus) in Stellenbosch Welgevallen Experimental Farm, with maximum CO_2 efflux occurred in summer (Keutgen et al., 2000). Mean seasonal soil respiration showed a strong seasonal rates of R_S and was parallel to that reported elsewhere (Rey et al., 2011) with rates of 0.80 and 1.10 µmol m^{-2} s^{-1} found in degraded and natural sites. However, Oyonarte et al. (2012) found that soil CO_2 effluxes were different in Natural Park (Spain) and showed a larger spatial variability in R_S with different behaviours between seasons of the years. However, it was lower than R_S rates reported in the savanna Okavango Delta (8 µmol m^{-2} s^{-1}, Mantlana 2008) and in tropical rainforest (Salimon et al., 2004).

Seasonal variability in R_S corresponded mostly with differences in soil temperature, soil moisture and plant traits during different seasons. Soil respiration is different between seasons and differed in the factors controlling CO_2 efflux during summer or winter. The decrease in soil CO_2 efflux at these sites occurs over a period in which the mean seasonal soil moisture was increasing, though soil temperature displayed a decreasing trend over autumn and winter measurement periods. Mean seasonal soil temperature under invaded sites decreased over the same time season. The inverse relationship found in summer between invasion statuses and landscape position phenology may modulate soil temperature at invaded sites (Phillips et al.,

2010). For example, during the summer, R_S may be responding to transport processes in the soil and therefore related to local factors such as root and the combined effect of both soil moisture and soil temperature. Thus suggesting the importance of vegetation, roots, and microbial biomass in understanding variable R_S patterns within invasion statuses (Raich and Tufekcioglu, 2000; Ma et al., 2005). This strongly suggests that studies of R_S should not only take into account the influence of environmental factors, but also incorporate biotic factors in order to scale-up the chamber measurements of R_S to ecosystem level.

We observed large and disproportionate changes in seasonal R_S between natural, invaded and cleared riparian sites within different periods in the fynbos of the south-western Cape. *Acacia* spp. was found to alter R_S rates through invasion statuses within the low-nutrient soils characteristically associated with the riparian fynbos ecosystems. Several sites in different biome have established a connection between photosynthesis and R_S (Högberg et al., 2001; Liu et al., 2009). Increase efficiency in water-use by *Acacia* trees due to higher photosynthesis play a key role in increasing both net primary productivity and gross primary productivity during dry periods (Sims et al., 2006; Way and Pearcy, 2012). The difference in R_S rates between invasion statuses were measured in the invaded sites and the lowest in the natural and cleared sites. The differences between invaded, natural and cleared sites were more pronounced in the dry periods. Mean values of R_S for summer ranged from 0.47-5.65 (μmol m^{-2} s^{-2}) for invaded sites, from 0.31 to 2.89 (μmol m^{-2} s^{-1}) for the natural riparian sites and about 0.22 to the 2.53 (μmol m^{-2} s^{-1}) for the cleared treatment but were all smaller than rates reported during the dry season in rainforests by Salimon et al. (2004) and in savanna by Mantlana (2008). Soil respiration rates found in our sites was parallel to that reported by Rey et al. (2011) whom found large differences in R_S between sites during spring, which coinciding with the highest level of plant activity and that there was not differences in R_S rates between the natural and cleared sites. The finding that R_S is different between riparian statuses and landscape positions support other studies reported in different ecosystems (e.g. Pacific et al., 2008; 2011), but did not support Phillips et al. (2010) results.

As hypothesized, our study indicates that R_S varied across riparian zones and adjacent terrestrial fynbos areas. These large variations in CO_2 effluxes mostly influenced by differences in invasion statuses, and associated seasonal patterns of R_S and landscape positions and morphology. Soil respiration was different from riparian zones to the terrestrial areas and was highest in invaded-riparian zones than in natural and cleared riparian sites. However, R_S in the riparian zones was no different in magnitude from wet to dry banks than did the terrestrial

zones. Generally, soil CO_2 efflux increased moving backward in the transects (dry banks-wet banks) ranging from 3.22 µmol CO_2 m^{-2} s^{-1} to 2.91 µmol CO_2 m^{-2} s^{-1}, and 2.69 µmol CO_2 m^{-2} s^{-1} in the terrestrial areas in summer. These results support the earlier study in complex riparian of the Rocky Mountains (North America) by Riveros-Iregui et al. (2011) and Pacific et al. (2009) who found higher rates of R_S across riparian zones. Natural and cleared riparian zones were similar and did not differ in their CO_2 efflux. This may be reflected the differences in plant cover and invasion statuses within micro-sites and the environmental factors. Over all, highest R_S rates occurred in summer 2011 during the dry season and the lowest in autumn and winter of both years. There was a positive effect of landscape position and *Acacia* spp. on R_S during different seasons. Riparian zones displayed an additional sharp in R_S response to landscape position and plant cover within or across wet banks, dry banks, and terrestrial zones. However, the variability in soil CO_2 efflux may exist in the landscape positions when measurements are combined over longer time periods, supporting the use of increasing CO_2 effluxes as a tool for invasion status within the landscape positions.

Root respiration and their associated microbial components are an important part of R_S in most ecosystems (Bowden et al., 1993; Kelting et al., 1998). While living roots directly contribute to R_S, dead roots and root exudates provide carbon as a source of energy and nutrients for microbial biomass. Grayston et al. (1996) reported that root exudates stimulate microbial growth and activity because they are easily digestible, and can these primers for the degradation of soil organic matter exists. These measurements were very similar to those measured elsewhere in temperate ecosystems by others (Jurik et al., 1991; Lessard et al., 1994) but different in the magnitude of R_S (Tufekcioglu et al., 2001). However, our results differed with R_S in red oak (*Quercus rubra*) and red maple (*Acer rubrum*) and *Pinus strobes* where CO_2 efflux was lower in wet land and higher in the terrestrial dried areas but simulated to seasonal increased in R_S with highest rates occurred in summer ranging from 4.6 (± 0.3) µmol CO_2 m^{-2} s^{-1} at the Harvard Forest Environmental Measurement Site, USA (Phillips et al., 2010).

Difference in magnitude between riparian zones and terrestrial areas may be explained by plant cover or plant density, which results in higher and more sustained soil CO_2 efflux and feedback to soil temperature and soil moisture. The lowest CO_2 efflux observed in the terrestrial areas during the course of this study may have been part due to lack of vegetation, low soil moisture, and landscape position, which become more drier and may be specific to fynbos due to intense fire previously occurred in these areas. Soil respiration responded differently to seasonal variation in soil moisture and GSWC as well as landscape positions so that mean seasonal R_S

rates was minimum in winter and maximum in summer and was different to that reported in Oak-grass savanna ecosystem in Californian (Tang and Baldocchi, 2005). We suggest that differences in R_S across the landscape positions were the result of decreased GSWC in 2010 during dry periods, during spring 2010 and summer 2011. For example, the frequency and timing of precipitation pulses, root mass, C/N ratio may be more important than the total amount of precipitation (Oyonarte et al., 2012; Almagro et al., 2009). Large increases in R_S (Lee et al., 2004) often follow precipitation events, the degree of which can vary with both rainfall frequency and type of vegetation (Fierer and Schimel, 2002), as well as antecedent soil moisture (Riveros-Iregui et al., 2008). It is known that in MTE's, rainfall pulses dictate microbial dynamics influencing CO_2 efflux (Fierer and Schimel, 2003; Xu et al., 2004). Increases R_S rates are much observed following dry conditions, even for the wet banks. Meanwhile, decrease soil CO_2 effluxes was associated with high soil moisture particularly in autumn and winter, with biogeochemical interaction between soil, root and microbial activities possibly even suspended. In 2011, there was a period of intense rainfall at the end of June, which may have inhibited R_S leading to drop in CO_2 efflux. The later peak in CO_2 efflux in the riparian zones during February 2011 may be due to increase gas diffusivity following the increase in soil temperature and reduced soil moisture (Lloyd et al., 1994). Dry season and intermediate soil moisture enable R_S, over all invasion status and landscape positions particularly in invaded-riparian zones, and this further confirms the fact that both temperature and moisture availability are very important R_S determinant in this part of the MTE's. Our results showed that both factors were good predictors for mean seasonal CO_2 efflux among our study sites. This result supports previous observations in which soil temperature and soil moisture in determining R_S in MTE's (Xu et al., 2004; Tang et al., 2005b).

The difference in the seasonal dynamics of R_S between invasion statuses could largely be explained by variation in plant activity. An influence of vegetation cover on R_S rates was also observed and larger variation in R_S among sites statuses was apparent, suggesting higher rates of R_S in invaded riparian sites were associated with woody *Acacia* trees. Soil CO_2 efflux generally increased with increases in litter mass, suggesting that aboveground productivity influenced R_S (Euskirchen et al., 2003; Burton et al., 2004). The significant relationships between R_S rates, root mass, litter mass and plant cover implies that heterotrophic respiration may become relatively more important than root respiration during certain seasons and is dependent on plant species (Palta and Nobel, 1989b; Poorter et al., 1995). Plant available mineral nutrients as well as nutrient content in plant tissues influence roots respiration. Kuiper

(1983) found that plant grown at high supply of nutrients have higher specific root respiration rates than plan grown at lower nutrient supplies. Furthermore, root respiration at certain temperatures may be higher during periods of high nutrient demand, example in summer and spring when vegetation grows fast (Bahn et al., 2006). Naudé (2012) showed higher concentrations in soils of invaded sites, which also supports the trend of higher R_S in richer soils, though the causal relationship between these factors are not apparent from this study.

In general, the presence of *Acacia* spp., in the riparian zones sustained higher rates of carbon cycling through the soil than did natural and cleared riparian sites. Although bulk density decreased under invaded sites but the greater pore space associated with reduced bulk density appear related to overall efflux as expected (Marchante et al., 2008; Oyonarte et al., 2012). Hanson et al. (2000) suggest a strong contribution of roots to total respiration depends on ecosystem type and seasonal patterns. In these degraded ecosystems, root mass and litter mass is greater in *Acacia*-invaded than in natural and cleared riparian ecotones. Respiration rate among plant species is variable in riparian fynbos. Fast growing plant species have higher respiration in comparison to slow-growing plants due to their lower specific respiratory costs of root growth and ion uptake (Poorter et al., 1991). Larger root mass has also potential to enhance root respiration and subsequently higher litter input offers more substrate for microbial respiration (Pregitzer et al., 2008). Root respiration decreases at low pH value ranged from 3-4 depending on species, when growth is inhibited and there is no adenosine triphosphate (ATP) demand (Yan et al., 1992). Salinity has also been shown to change the relative contribution of root versus microbial soil respiration; at higher soil salinity levels (here represented by higher electrical conductivity levels; Naudé 2012), similar to what was found by Garcia and Hernandez (1996) and by Garcia et al. (2002). When plant growth is inhibited at very high levels of salinity subsequently also soil respiration decreases.

Differences in soil organic matter such as litter input across riparian sites likely influenced the observed variability in riparian zones (Ju and Chen, 2005). These variations were potentially influenced by differences in drivers R_S, root mass, geomorphology slopes and attributes. Soil respiration rates correlated with litter input and root density. High R_S rates across *Acacia*-invaded sites riparian zones are due to more fine roots leading to higher CO_2 efflux. *Acacia* trees mostly *A*. *mearnsii* invades the low land part of riparian areas in both wet and dry banks. However, alien plants were much prominent in the dry banks as reported in previous study (Boucher 2002). Root mass present a larger impact than surface litter in soil CO_2 efflux values but are both crucial and major processes in the carbon and nutrient dynamics of the riparian

ecotones (Vogt et al., 1982; Vargas and Allen, 2008). Results showed that invasion statuses caused low structure complexity with high significant increase in root density, aboveground litter mass and lower bulk density in riparian zones investigated. Hence the contribution of alien plants invaders of these ecosystems to total R_S decreased soil carbon stock and carbon balance in riparian zones. The magnitude of R_S CO_2 efflux obtained in this study is consistent to that reported for central Montana (Pacific et al., 2010), similar for a mixed-conifer forest MTE's, under deciduous oaks in California (Ma et al., 2005; Tang and Baldocchi, 2005). These increased in R_S may be the combination of soil texture flushing of soil pores as supplement air CO_2 is replaced by water, a fast response of microbial activity that is possible from persistent pool of enzymes able of tolerating extending periods of desiccation and were high than that reported in arid succulent Karoo South Africa, Nyaga (2009) and to that reported for California under different land-use (Tang and Baldocchi, 2005). However, a novel aspect of this investigation was the integration of alien plants and seasonal measurements of R_S with detailed observation of soil temperature and soil moisture using invaded-riparian fynbos ecosystems.

Fynbos R_S rates are dependent on the riparian type and treatment applied. We explored the use of R_S as an indicator of riparian functioning reflecting changes in plant species due to leguminous *Acacia* trees invading to Mediterranean fynbos riparian ecosystems. To our information, there has been no other study that has examined seasonal variation of R_S between different invasion statuses and within landscape positions in MTE's of the south-western Cape. Riparian and adjacent fynbos CO_2 effluxes are dependent on the ecosystem type and status. The outcome of this study supports our hypothesis that R_S is different among site with different invasion statuses is different within landscape positions, but this depends on the season. The effect of *Acacia* and landscape position on R_S is dominant. Our results show that higher R_S rates were associated with both environmental factors and vegetation cover; higher invasive cover meant higher R_S. Soil temperature and soil moisture may influence the change in aboveground root in different ways in natural, invaded and cleared sites. Soil moisture and temperature was an important control during drier and warmer seasons, with these relationships most prominent in invaded riparian zones. Furthermore, *Acacia* spp. at invaded riparian sites tends to have greater number of fine root and greater aboveground litter than the natural and cleared sites. Soil CO_2 efflux was positively correlated with cover of alien seedling and young plants. We observed a pulse of R_S in invaded dry banks during summer season compared to wet seasons. Lowest R_S rates were observed during wet season and also within natural and cleared sites, however, highest CO_2 effluxes were found during the dry season.

2.7 CONCLUSION

Soil respiration and carbon cycling in invaded-riparian ecosystems may play an important role in monitoring restoration as *Acacia* trees increase soil carbon, nitrogen deposition and basal respiration (Marchante et al., 2008). Our results give clear indications that there is significant spatial heterogeneity in R_S and root mass dominates the small-scale spatial pattern of R_S. This phenomenon also suggests that the spatial variation in biotic factors and soil features should been taken into account in order to accurately estimate R_S. We found that interactions among soil temperature, GSWC and root mass largely control the seasonal and temporal variation in R_S during the growing season. This strongly suggests that the studies of R_S should not only take into account the influence of environmental factors, but also incorporate biotic factors in order to scale-up the chamber measurements of soil respiration to ecosystem level, which could undoubtedly lead to an improvement in predictive capabilities of the model. Our results showed that, clearing after *Acacia* spp. invasion is crucial in restoration ecology as changes in riparian ecosystems modify R_S and soil carbon balance, but that clearing apparently restores soil functioning, at least as far as soil respiration is concerned. Oyonarte et al. (2012) identified R_S as good indicator of an ecosystem status. Therefore, R_S may be used as an important tool for monitoring of restoration of riparian functioning in the fynbos area. Partitioning R_S into autotrophic and heterotrophic respiration of below and aboveground activity could provide insight into the mechanisms necessary underlying trends of respiration in invaded riparian ecotones, and is an important next step to enhance our understanding of soil carbon dynamics in fynbos riparian and upland environments, and especially regarding invaded and cleared areas.

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CHAPTER 3

THE RELATIVE IMPORTANCE OF AUTOTROPHIC RESPIRATION TO OVERALL SOIL RESPIRATION RATES IN *ACACIA*-INVADED RIPARIAN ECOTONES, AT DIFFERENT LANDSCAPE POSITIONS

3.1 ABSTRACT

Soil respiration (R_S) consist of a group of complex and interconnected processes which involve plants, soil microorganism and soil fauna. Typically, soil respiration consists of faunal respiration, usually around 10 %, whereas plant roots and soil microbial respiration produce the largest portion (90 %). Many riparian ecosystems in south-western Cape are invaded by the leguminous tree *Acacia mearnsii* and other *Acacia* spp. Invasive N-fixing plants species have been shown to affect carbon and soil nitrogen input, plant growth and community dynamics. In this study the impact of invasion by Australian *Acacia* spp. on autotrophic and heterotrophic respiration is investigated by using incubations of soil at constant temperature and moisture (potential soil respiration; PR_S), as well as trenching to investigate root respiration's contribution to overall soil respiration. We compare fluxes to soil and trenches in natural fynbos riparian ecotones and uplands (reference) and to cleared riparian ecotones where *Acacia* spp. has been cleared 7 years prior to the commencement of the experiments, and we also carried out sampling at different landscape positions. All invaded sites had higher root mass; litter mass and lower C/N ratio compared to the natural and cleared riparian ecotones. However, little differences between sites with different invasion status were evident when measuring CO_2 emission over time. Although it appeared that invaded sites had higher PR_S, this was not statistically significant ($F = 0.76$; $P = 0.063$). Also, while it appeared that PR_S was highest in dry banks, this was not consistently significant ($F = 16.32$; $P < 0.05$). However, when root mass was determined, we found higher roots mass in invaded dry banks. Further, trenching of soils in invaded dry banks lead to a major decline in R_S, and though the differences in CO_2 efflux rates later disappeared, possibly as a result of decomposition of fine and coarse roots. We think that enough evidence has been shown to conclude that it is root respiration, rather than microbial respiration that is most influential in driving overall soil respiration.

KEYWORDS: Roots, microbes; Invasive alien plants, Trenching; Decomposition; efflux;

3.2 INTRODUCTION

One of the major fluxes in the global carbon cycle is the uptake of CO_2 by plants as photosynthesis (Benjamin 2006). On the other hand, the soil is the largest terrestrial carbon pool (Post et al., 1982). Bowden et al. (1993) defined soil as pools of carbon storage that annually release enough carbon to influence global carbon cycles, while soil respiration (R_S) is the largest component of ecosystem respiration (Ryan and Law, 2005). Soil consists of a number of distinct fractions that store different amounts of carbon and their variation depend on sensitivity to changes in environmental variables. Overall, R_S accounts for the release of about 60Pg of carbon in the form of CO_2 per year (Schimel et al., 1995). This figure is more than 10 times the total annual carbon release due to anthropogenic sources (Trumbore and Harden, 1997). An increase in the average surface temperature of the planet over the century of about 2.5 °C is predicted by computer models, mainly due to anthropogenic changes in carbon fluxes (Houghton et al., 1996). This increase has the potential to substantially increase the rates of R_S (Raich and Schlesinger, 1992; Andrews et al., 1999), thus a positive feedback loop. Since CO_2 efflux constitutes 60 % of greenhouse gas if water vapor is not considered, understanding its flux becomes very important in relation to global warming. Increased R_S again contributes to the positive feedback loop that could further increase the temperature of the earth's surface (Kirschbaum 1995).

Soil respiration is the sum of plant root, animal and microbial respiration. A major challenge is the separation of the soil CO_2 efflux into heterotrophic respiration and autotrophic respiration. We define autotrophic R_S as the sum of an autotrophic component produced by roots and the associated rhizosphere and heterotrophic component originating from soil microorganisms that decompose the organic materials from both above and belowground litter (Kutsch et al., 2009; Kuzyakov et al., 2006; Eliasson et al., 2005; Soe et al., 2005; Epron et al., 2001). In comparison to the microbial respiration, using photosynthate as substrate, root respiration is a direct and faster route of carbon release, which is fixed by plants through photosynthesis (Cheng et al., 1993; Högberg and Read, 2006). In contrast, microbes use organic matter shed by plants and other biota and release CO_2 through respiration, which is thus a more circuitous and also a longer term route for carbon release.

Studies in different ecosystems around the world showed plant roots to contribute about 10 to 90 % of total R_S, depending on vegetation type and season of the year (Hanson et al., 2000). Kudeyarov and Kurganova (1998) noted that in most cases, half of total R_S is autotrophic.

Partitioning R_S is essential for calculating the carbon budgets of vegetation components of an ecosystem and understanding sources and sinks of carbon in the face of global climate change (Högberg and Read, 2006). The distinction between R_S components is also important because the activity of soil heterotrophic organisms is proportional to the decomposition of SOM and the autotrophic fraction (respiration of roots, mycorrhiza and associated bacteria) dependent on the supply of recent photosynthates (Millard et al., 2008; Högberg and Read, 2006; Högberg et al., 2001). However, Epron et al. (2001) found that R_S from rhizosphere components fluctuated between 30 to 60 % in Mediterranean beech forest, while Jiang et al. (2005) found roots to contribute 25 to 65 % for a mixed stands in a larch plantation. Between 49 to 57 % of total R_S was found to come from root respiration in cedar forest (Ohashi et al., 2000), and 27 to 71 % in a deciduous forest (Lee et al., 2003). However, these rates were not associated with seasonal variability and may vary during the growing season (Hanson et al., 2000). However, partitioning root and microbial respiration under field conditions is still complicated. The interaction between the rhizosphere and the surrounding soil complexity makes it difficult to determine the different components of R_S, as any trenching approach to separate the components will necessary disturb these interactions (Kuzyakov and Larionova, 2006; Subke et al., 2004; Lee et al., 2003; Ekblad and Högberg, 2001). Also, varying environmental conditions makes repeatability of experiments to assign sources a challenge (Trumbore 2006; Reichstein et al., 2005, 2008).

Soil respiration is influenced by plant root characteristics via its impacts on root respiration (Kuzyakov et al., 2000). Autotrophic respiration is influenced by factors including root diameter (Pregitzer et al., 1998; Andrews et al., 1999), nitrogen and total nonstructural carbon content (Burton et al., 2002; Desrochers et al., 2002), root function, and root depth (Pregitzer et al., 1998; Bhupinderpal et al., 2003). Environmental conditions such as biotic (Symbiotic and parasitic organisms) and abiotic factors also influence root respiration as well as nutrients supply (Lambers et al., 1991), such as temperature (Bond-Lamberty et al., 2004; Maier and Kress, 2002) as well as season (Vose and Ryan, 2002) but rhizobium is one example of symbiotic organisms which create nodules on roots and supply fixed atmospheric N. On the other hand, the main factors that controlled heterotrophic respiration are water content, temperature, oxygen (O_2) alternative electron acceptor availability, organic matter availability as well as the availability of nutrients. Site characteristics (soil pH and texture) also influence soil CO_2 efflux due to their direct effect on carbon turnover rates and diffusion of CO_2 (Jensen et al., 1996; Howard and Howard, 1993). Microbial activity depends on plant organic matter in the soil, the quality of which varies depending on the plant species composition and plant productivity

(Waldrop and Firestone, 2006). The autotrophic component is then obtained by subtracting heterotrophic respiration of root-free respiration and applying a number of corrections. However, studies that have addressed the issue of quantifying R_S into autotrophic and heterotrophic respiration have shown that CO_2 efflux rates are highly variable from one season to another and depend on ecosystems (Yi et al., 2007; Díaz-Pinés et al., 2010).

Root and their microbial symbionts are responsible for most of the nutrient uptake in legumes but they are also major sink for plant photosynthates (Paul and Kucey, 1981; Jacobsen and Rosendahl, 1990). Mycorrhinzal fungi usually promote plant growth by improving plant uptake of P and other immobile nutrients (Smith and Read, 1997). Rhizobial bacteria form symbiotic associations with legume species and fix atmospheric N_2. This process has high phosphate (ATP) and photosynthate requirements and has been stimulated by mycorrhizae and P fertilization in various studies (Barea and Azcón-Aguilar, 1983). Mycorrhizal and rhizobial functioning are therefore linked to each other in legume species. Furthermore, it has been hypothesized that the continuous removal of C compounds for mycorrhizal and rhizobial growth and activity increases sink strength (Pang and Paul, 1980) and prevents the accumulation of photosynthates in the leaves which could, in turn, lead to down regulation of photosynthesis (Harris et al., 1987). Increased sink activity may increase plant photosynthetic rates and the amount of carbon allocated belowground (Harris et al., 1987; Tufekcioglu et al., 1999). The tripartite association would then have optimal performance at elevated CO_2 with a combination of enhanced root activity. Symbiotic N_2 fixation has increased at elevated CO_2, and this amplified the plant growth response to additional C availability (Hartwig 1998). However, there is increasing evidence that elevated CO_2 has little effect on mycorrhizae development and functioning (Staddon et al., 1999a, b; Staddon and Fitter, 1998), although there may be some fungal interspecific differences to consider (Klironomos et al., 1998).

Most studies on factors controlling R_S have either focused on temperature and soil water content in terrestrial landscapes in different ecosystems (Bond-Lamberty et al., 2011; Lee et al., 2003), and only a few have explored the contribution of root respiration to total R_S in wetlands (Jauhiainen et al., 2012; Špátová 2011). Given the projected decreases in precipitation and temperature increase for MTE's (Kueppers and Harte, 2005; Scott-Denton et al., 2006), it is particularly important to understand how both heterotrophic and autotrophic components affect total R_S. However, autotrophic and heterotrophic respiration are linked due to the interaction of controlling factors that may affect these components differentially in space and time (Hanson et al., 2000). This makes it complex to separate their respective activities *in situ*, especially since

organisms in the rhizosphere may be partly autotrophic and heterotrophic, and may vary temporally in this respect (Högberg and Read, 2004, 2006; Elisabeth et al., 2005). Therefore, determining root excluded R_S need as much attention as possible and has been the aim of numerous studies using different techniques, each with their own advantage and disadvantage and underling hypothesis (Epron et al., 2001; Bowden et al., 1993). In previous studies, the estimates of root respiration varied from a minimum of 4 % (Phillipson et al., 1975) to a maximum of 62 % (Ewel et al., 1987) of the total R_S. In addition, variability in R_S was found best predicted by the amount of living fine roots in a variety of Oregon forests (Campbell et al., 2004). It is not entirely clear how the contribution of the various components of R_S varies at the landscape level, and the relative importance of different controls.

Riparian zones in the fynbos are crucial for providing various ecosystems services, e.g. clean water, but are also highly degraded due to various anthropogenic drivers. Alien invasive species are a major factor leading to riparian degradation, and alien invasive plants such as *Acacia mearnsii*, *A. longifolia*, *Eucalyptus* spp. and *Pinus* spp. have been declared weeds and a major ecosystem restoration initiative, the Working for Water program instituted to clear these woody species and restore ecosystem services. It is now known that the invasive *Acacia mearnsii* and other riparian *Acacia* spp. increase R_S, but this is a seasonal trend (Kambaj 2011), however, it is unclear what component of R_S contributes the most. Although partition of autotrophic and heterotrophic respiration is very crucial issue (Vogel et al., 2005a; Millard et al., 2008; Millard and Grelet, 2010) for the improvement of our understanding on the effect of IAPs on soil CO_2 efflux and balances it is worth mentioning that to date it has not been addressed for this Mediterranean-type ecosystem.

The current study is the first to our knowledge to investigate the responses of seasonal R_S without roots and with root in invaded-riparian ecotones to estimate heterotrophic respiration and autotrophic respiration in the field and under controlled conditions owing IAPs. The main objective of this study was to determine autotrophic and heterotrophic respiration's contribution to total R_S. The main question addressed in this part of the study is:

- What is the relative contribution of root respiration to overall R_S?
- How does this differ between sites with different invasion status?

3.3 MATERIALS AND METHODS

3.3.1 Site descriptions

For the *ex situ* measurement of R_S (potential R_S), soil was sampled from sites in the Western Cape (the same ones as for the *in situ* measurements; as shown in figure 2.1) and the Southern and Eastern Cape (sites used exclusively for the *ex situ* measurements). The sites from the Southern and Eastern Cape were all within the fynbos biome, and chosen as a second series of sites used to verify some of the trends obtained from the Western Cape sites.

In the Southern and the Eastern Cape we samples soil around the towns of Haarlem and Kareedouw. The details of each site are given in Table 3.1. For the Western Cape sites the detailed descriptions are as given in Chapter 2, however, a short summary of the Western Cape sites is also given in Table 3.1.

Table 0.1: Description of sites from where soil was collected and trenches installed.

	Site name	Coordinate	Invasion status	Location	Vegetation	
Southern and Eastern Cape	Baviaans River	33˚48.706S; 024˚25.832 E	Restored-active restoration	Kouga Mountain	Fynbos	Soil collected for *ex-situ* incubation
	Voeght's River	33˚46.496S; 023˚09.368 E	Natural	Langkloof	Fynbos,	Soil collected for *ex-situ* incubation
	Voeght's River	33˚46.496S; 023˚09.368 E	Natural	Langkloof	Fynbos, Restionaceae	Soil collected for *ex-situ* incubation
	Witteklip River	33˚49.782S; 024˚26.932 E	Invaded	Kouga Mountain	*A*. *mearnsii*, Restionaceae, forbs and grasses	Soil collected for *ex-situ* incubation
	Kammanassie	33˚42.296S; 023˚09.623E	Invaded	Langkloof	*A. mearnsii/A. dealbata*	Soil collected for *ex-situ* incubation
	Groot River	33˚43.392S; 023˚22.420 E	Invaded	Langkloof	*A*. *mearnsii*, *A*. *dealbata*, *A*. *longifolia*,	Soil collected for *ex-situ* incubation
	Witteklip River	33˚49.713S; 24˚26.699 E	Cleared	Kouga Mountain	*A*. mearnsii,	Soil collected for *ex-situ* incubation
	De Hoop	33˚42.060S; 023˚09.383 E	Cleared	Langkloof	*A*. *mearnsii*, *A*. *dealbata*, *A*. *longifolia*,	Soil collected for *ex-situ*

	Site name	Coordinate	Invasion status	Location	Vegetation	
					Restionaceae, forbs and grasses	incubation
	Groot River	33˚43.392S; 023˚22.420 E	Cleared	Langkloof	*A*. *mearnsii*, *A*. *dealbata*, *A*. *longifolia*, forbs and grasses	Soil collected for *ex-situ* incubation
Western Cape	U. Eerste River	33°57.136 S; 18°58.438 E	Natural	Jonkershoek	Fynbos	Soil collected for *ex-situ* incubation
	L. Eerste River	33°59.222 S; 18°58.037 E	Natural	Jonkershoek	Fynbos	Soil collected for *ex-situ* incubation
	U. Dwars River	33°57.160 S; 18°58.4778 E	Natural	Kylemore	Fynbos	Soil collected for *ex-situ* incubation
	Wit River	33°32.185 S; 19˚0.556 E	Invaded	Bainskloof	A. *mearnsii*	Soil collected for *ex situ* incubation; trenches dug
	L-Dwars River	33˚57.160S; 18˚58.477 E	Invaded	Dwarsberg Mountains, at Kylemore	*A. mearnsii and A. longifolia*	Soil collected for *ex situ* incubation; trenches dug
	L-Jakkals River	33˚12.318S; 19˚10.387 E	Invaded	Bot River farm/Kleimount	*A. mearnsii and A. longifolia*	Soil collected for *ex situ* incubation;

Site name	Coordinate	Invasion status	Location	Vegetation	
					trenches dug
L. Molenaars	33˚42.385S; 19˚11.492 E	Invaded	Du Toits Kloof Mountains/Rawsonville	*A. mearnsii*	Soil collected for *ex-situ* incubation
Sir Lowry River	34˚05.415S; 18˚56.397 E	Cleared	Wedderville Estate	Restionaceae, forbs and grasses	Soil collected for *ex-situ* incubation
U. Jakkals River	33˚13.011S; 19˚12.258 E	Cleared	Bot River farm/Kleimount/ CapeNature	Restionaceae, forbs and grasses	Soil collected for *ex-situ* incubation
U. Molenaars	33˚42.169S; 19˚13.594 E	Cleared	Du Toits Kloof Mountains	Restionaceae, forbs and grasses, A. *mearnsii*	Soil collected for *ex-situ* incubation

3.3.2 *Ex-situ* soil respiration and soil sampling and incubation

Composite soil samples were collected in the riparian zones and upland areas within nine different sites in the south-western Cape from the Eastern and Southern Cape (January and June 2011). Ten soil cores were collected using a stainless steel core soil sampler (4.5 of internal diameter) inserted into the upper part of soil profile at 0-10 cm depth and bulked in the field. Bulked soils were kept transferred into in labelled plastic bags and transported to the laboratory in a cooler box and stored in a refrigerator at 4 °C prior to the further processes. Soil samples were air-dried inside the laboratory at ambient temperature for about 4 to 5 days. Soil lumps were gently crushed. Gravel particles, roots and coarse debris were removed by hand and finally sieved through a 2 mm mesh sieve. This ensured that it was free of any large pieces of root or other organic and inorganic material. To ensure that soils were well settled before measurement, the microcosms were left equilibrated for one or two hours before taking the first CO_2 emission measurement.

Measuring of CO_2 efflux (potential soil respiration; PR_S) was done under the laboratory controlled conditions. Microcosms vessel consisting of polyvinylchloride (PVC) piping, and were 13 cm deep x 10cm diameter. Containers were filled with soil from the study sites (600 g) adjusted to 60 % water holding capacity soil (WHC). The bottom and the top of each microcosm was also covered with a cap made of the same opaque materials as the PVC tubing and sealed with silicon to ensure that water and gas leakage are minimized. To avoid any gas diffusion from the silicon and the PVC material itself, before placing soils into the microcosm, the empty vessels were washed in hot water at 120 ºC then tested (CO_2 efflux). Microcosms were left for one day in the laboratory to allow the soil to settle before being moved into the incubator room. Microcosms were maintained in a dark temperature-controlled environmental room at 30 °C for four weeks. Soil inside microcosm was maintained at about 60 % WHC by wetting soils prior to measurement. Determination of the GSWC of the sieved soils allowed calculation of WHC of the soils sample and hence the amount of drying and rewetting soils to adjust the soils to 60 % (Garretson 1999; Paul et al., 2001). Gravimetric soil water content (% by weight) was calculated using the following formula: [GSWC= ((Wm-Dw) / Dw) x 100]. Where (Wm) is wet mass express in gram and (Dw) is the dry weight in gram.

CO_2 efflux measurements were conducted on weekly basis (day 1, day 7, 14, and day 28); changes in microcosm mass were used to determine water loss. Additional distilled water was added after each measurement, should it be required, to maintain constant moisture levels over

the entire periods of soils into incubation. In the incubation room, soils microcosms were placed on 100cm x 200 cm wooden table and incubated in the dark at 30 °C. No amendments other than distilled water was made to any of the microcosms.

3.3.2.1 Soil CO_2 emission measurements

An infrared gas analyzer, Li 8100 model, (Li-Cor Biosciences), was used to measure soil CO_2 emissions. The IRGA response to CO_2 emission was calibrated against prepared standards of 380 and 630 ppm µmol/mol CO_2. The instrument was allowed a 30-minute warm-up time, after which it remained on for the duration of measurements. Potential CO_2 measurements required 2-5 min (circulation time) before recording were done. Two empty PVC vessels were used as blanks. The soil inside the microcosm was representative of soil collars in the field, in terms of dimensions and depth of soil sampled. It took approximately four to five hours to complete the first cycle.

We measured potential R_S as CO_2 emission µg CO_2-C.g $soil^{-1}$ d^{-1} every 7 days, starting with day 1. To avoid pulses of CO_2 due to pressure fluctuations created by opening and closing lid, the measurement interval was reduced to that with minimal pressure fluctuations. Distilled water was added to microcosms weighing less than the original weight in order to maintain soils at 60 % water holding capacity. Once the first measurements were taken on day zero (data not shown) at ambient temperature in the laboratory, soil microcosms (PVC pots) were then transferred to incubation room where temperature was constant for ongoing measurements. We measured PR_S for CO_2 carbon efflux for the incubation period and calculate carbon mineralization rate, expressed as µg CO_2-C.g $soil^{-1}$ d^{-1} according to the formula modified by Robertson et al. (1999):

$$F = C_{rate} \text{ X } V/A \text{ or } W$$

where: F = carbon mineralization rate, expressed as µg CO_2-C.g $soil^{-1}$ d^{-1}

C_{rate} = change in CO_2 concentration over the incubation period, calculated by regression C_m

(µg CO_2-C.g $soil^{-1}$ d^{-1}) vs. incubation time (d)

V = headspace volume of microcosm vessel (L)

A = surface area represented by soil in microcosm

W = dry mass of soil in microcosm (g)

3.3.2.2 Trenching

Partitioning R_S rates with the root exclusion approach is a straightforward way to measure CO_2 efflux without roots on relatively disturbed soil using standard surface flux techniques. It can be applied in a variety of ecosystems, although it may require extensive labour and root barriers in locations with deep soil. This experiment was begun in October 2010 as a secondary study to separate out root respiration from total soil respiration in situ. The approach aims to exclude roots from soils by digging and installing a thick plastic sheet barrier vertically into the soil and then measuring respiration in and outside the root exclusion plots. The method is called the root exclusion method or as the trenching method (Hanson et al., 2000; Vogel et al., 2005; Bahn et al., 2006). This technique provides an estimate of root and mycorrhizal respiration in reference to microbial respiration inside the exclusion area. The weakness of this technique is strong disturbance of soil during trenching operation, potential alterations to the C and N cycle, alterations to soil moisture dynamics and changes to root and organic matter decomposition (Davidson et al., 2000; Kuzyakov 2006; Vargas et al., 2010). This is because soils are dug up and disturbed and roots are cut off and all roots remain in soil and where a physical barrier is installed to prevent roots growth out the soil block.

Figure 3.1: Photos of root exclusion (trenched plots) dug in the invaded dry banks at the Wit River site in Bainskloof. The first picture (A) is of a trench, showing the high root densities, and the second photo (B) shows the plastic sheeting 4 mm thick x 6 m in length used to exclude roots from the central soil block with PVC collar inserted into the soil in the center of trenched plot for CO_2 emission measurements.

We set up a series of 1x1 m by 0.5 m (depth) plots in ≥ 10-year Acacia-stand in fynbos riparian zones (dry bank only) as shown in figure 3.1A. The three sites chosen were all invaded sites the Dwars River site, the Jakkals River site and the Wit River site. Thirteen trenches were dug outside of the plots used for general purpose sampling (including the original soil collars for soil respiration measurements) and roots were excluded with heavy-duty polyethylene plastic sheet (4mm thick x 6m in length) which was wrapped on the outside of a relatively undisturbed central soil block (see figure 3.1) in order to prevent growth of roots into the block soil plots (Figure 3.1B). Hereafter the trenches were refilled, where after CO_2 efflux measurements were conducted inside and outside the root exclusion plot (Bowden et al., 1993; Lavigne et al., 2003; Wang et al., 2005). PVC collars (10cm of inner diameter) for CO_2 efflux measurements were inserted to a depth of 4cm, on control and root exclusion plots. Collars insertion was done on the same day after trenches were dug (Figure 3.2B). Overall, the plot edges where 2 m apart from each other. Understory vegetation within and immediately surrounding all plots was removed seasonally throughout the study (Burton et al., 2002). However, given that the 0.5 m root barriers were already isolating these areas from roots of nearby trees, the majority of live roots in these plots would have been from herbaceous understory vegetation (mostly grasses, Restionaceae, and forbs). Soil disturbance was thus kept to a minimum.

Soil respiration measurements were made four months later in February 2011, to allow trenches to equilibrate after disturbance occurring during trenching processes. Carbon dioxide (CO_2) efflux from the soil surface was measured using an LI-8100 (IRGA) an automated system, (LI-Cor Inc., Lincoln, NE, USA) with incorporate soil chamber. This system consists of a portable IRGA connected to a laptop computer and each measurement takes 2 min observation time. All measurements were done in 2011 and once in 2012, and were done on a season basis once in mid-summer, early autumn, mid-winter from June to July, and for two weeks in spring from late August to late September. One set of spring measurement was done inspiring 2012 in order to test where the trends observed in 2011 were still present. We measured R_S on both intact control and on without root or root exclusion plots between 09h00 to 16h00. Soil moisture and temperature measurements were also carried out at the same time as the CO_2 efflux measurements and samples taken for GSWC; these measurements were carried out in the same way as for the in situ measurements described in Chapter 2.

3.3.3 Determination of root mass and selected soil properties

Few soil characteristics such as bulk density, root mass, and litter mass were assessed. Soil moisture was determined gravimetrically by drying the samples. The weight of water was estimated as the difference between the weight of the sample and its weight after oven drying at 110 °C for 24 hours. Soil pH and electrical conductivity (EC) were not measured due to time and study schedule. Biomass of fine roots was collected from the core using a 15cm tall and 4.5 diameter samplers. Roots sample were manually assessed in the laboratory, washed with distilled water then oven dried at 60 °C. Litter mass were collected using a 25 cm^2 wooden frame. In the laboratory, the litter mass was weighed and oven dried at 70 °C. Plant and belowground cover were assessed by considering the vegetation or aerial cover (canopy) and soil cover within the study areas.

3.4 DATA ANALYSIS

The effects of the two different treatments (control and trenching) on total R_S rates were compared to the treatment within landscape position and comparisons among means were made across seasons and treatment using the least significant difference (LSD) test calculated at $P < 0.05$ using analysis of variance (ANOVA) as provided in the program Statistica (StatSoft, Inc, version 10.0.). For PR_S, invasion status, landscape position and season were fixed factors and grouped in sites with sites as random factor. Nevertheless, fixed factors were used as the main effects and differences between individual sites were not tested. When interacted with treatments and landscape positions (wet, dry banks and terrestrial areas) across invasion status within group were tested with repeated ANOVA and a post hoc test was applied when necessary. We used data from 9 (x 2) sites in the analysis although invasion is most established in riparian dry bank zones. But when tested across invasion status one-way ANOVA was used for difference between treatment and landscape position. The effect of invasion status and treatment, soil bulk density, litter mass, and root mass was also tested using LSD test (StatSoft, Inc, version 10.0.228.2).

3.5 RESULTS

3.5.1 Potential Soil Respiration

Our approach permitted us to estimate PR_S rates using water only as amendment without other substrates, while incubation took place at a constant temperature (30 °C). Potential R_S rates ranges from 0.91 to 2.10 PR_S µg CO_2-C.g $soil^{-1}$ d^{-1}, with the maximum values obtained on day

14, and was 2.16 µg CO_2-C.g $soil^{-1}$ d^{-1}. Soil from southern and Eastern Cape riparian ecosystems showed similar R_S rates overall, with little major differences in landscape position and invasion statuses. Potential R_S rates varied depending on the sampling date (Figure 3.2). Potential R_S in invaded riparian sites tended to be the highest when measurements were taken in day 7 in the samples from the Western Cape and day 14 in those from the Eastern Cape.

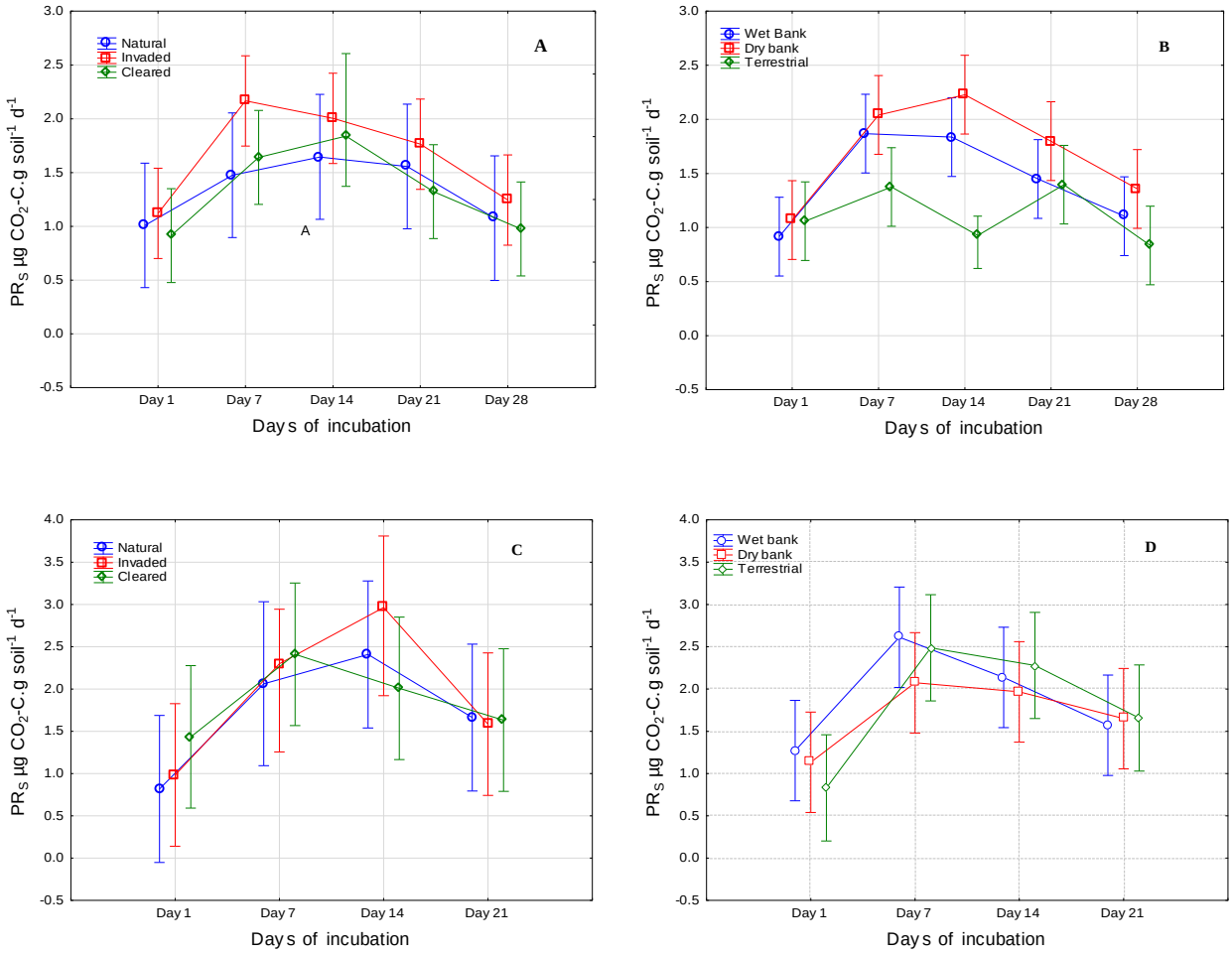

Figure 3.2: Potential soil respiration (PR_S: µg CO_2-C.g $soil^{-1}$ d^{-1}) measured by invasion statuses (Figures A and C) and by landscape positions (Figures B and D) during incubation on day 1 to day 28. Soils used for incubation were sampled from the south-western Cape sites (A and B), and from the Eastern Cape sites (C and D).

While PR_S of the soils from the invaded sites declined over the course of the incubations (both regions), it remained the highest of the three sets of samples (natural, invaded, and cleared), though there was not a statically significant difference (Table 3.2). Regarding the landscape positions, incubated soils from the dry banks in the Western Cape tended to have higher R_S, and had statistically higher PR_S rates than the terrestrial sites (Table 3.2). Little differences emerged in the PR_S values for the Southern and Eastern Cape.

Table 0.2: ANOVA statistics for potential soil respiration (PR_S) measured during the course of incubation, invasion status versus landscape position, invasion status and landscape position versus period of measurements. CO_2 efflux in µg CO_2-C.g $soil^{-1}$ d^{-1}. Data are from the south-western and the Eastern Cape riparian sites. (DF: Degrees of freedom, F: Statistics, P: Probability F value at $P < 0.05$. n.s indicates non significance, *: significant indicates significant at $P < 0.05$.

Incubation (Western Cape)	**Source**	**DF**	**F**	***P*-values**	**Significance**
Time of measurement	PR_S	28	5.99	0.001	*
Invasion status	PR_S	7	4.65	0.051	*
Invasion status X Landscape position	PR_S	44	1.15	0.003	*
Landscape position	PR_S	11	16.32	0.000	*
Invasion status X time of measurement	PR_S	28	0.76	0.063	ns
Landscape X time of measurement	PR_S	44	10.19	0.000	*
Incubation (Eastern Cape)					
Time of measurement	PR_S	18	12.35	0.000	*
Invasion status	PR_S	11	0.15	0.085	ns
Invasion status X Landscape position	PR_S	33	0.81	0.063	ns
Landscape position	PR_S	11	0.44	0.014	*
Invasion status X time of measurement	PR_S	18	0.71	0.064	ns
Landscape X time of measurement	PR_S	33	1.05	0.041	*

3.5.2 Root mass and litter mass

Significant differences were observed at ($P < 0.05$) for any of the determinant of litter mass and root density for their interaction between invasion statuses and landscape position (Table 3.3). Invasion status and landscape position litter and root density were significantly greater ($P < 0.05$) for both regions under *Acacia* stands than that of natural riparian sites and *Acacia*-cleared. There was a difference between riparian statuses ($F_{[8, 324]} = 2.27$, $p = 0.02$). Compared to the Western Cape, root mass was higher in the Eastern Cape with 22 versus 16 Kg m^3 (invasion status; Table 3.3). We observed a slightly differences at landscape positions where the Eastern Cape riparian ecosystems had lower root mass and remained highest in litter mass than the Western Cape and significant in the wet banks and dry banks for both regions ($P < 0.05$). This difference was mainly due to much higher root density of the very fine roots in the litter and upper 10 cm of the mineral soil (Eastern Cape sites) as well as the *Acacia* trees density. Our observation during trenching showed that, root proliferated in these dry banks of the nutrient poor zones in the soil and large spatial variability in root production was therefore expected. Also the lateral distribution of *Acacia* root growth and biomass may be probably related to nutrient ease of use. *Acacia* trees typically accumulate a thick layer of litter in which large amount of nutrient are stored. Suggesting that, fine roots tend to concentrate in and just below this large source of nutrient.

Western Cape and Eastern Cape characteristics of the invasion statuses riparian sites were similar for both regions along natural, invaded, and cleared riparian ecosystems, see Table 3.3, for means and standard errors. Bulk density was lower for the invaded sites and higher in the natural and cleared sites depending on the riparian sites and status and was significantly different (Table 3.3; $F_{[2, 13]} = 4.45$, $p = 0.03$). Landscape position was different in bulk density with dry banks having lower bulk density than wet banks and terrestrial zones for both Western Cape sites than the Eastern Cape region.

Table 0.3: Initial aboveground and belowground litter mass, bulk density and root mass elements. Values are means with standard errors in parenthesis. Different superscript letters indicate significant differences ($p < 0.05$) between potential soil respiration and trenching. ANOVA was used to indicate differences between landscape positions and invasion status. S.E.C: Southern and Eastern Cape and W. C: Western Cape. L: litter mass (kg); BD: Bulk density (g soil cm^{-3}); RD: Root density (kgm^3).

		Natural	Invaded	Cleared	Wet bank	Dry bank	Terrestrial
S.E.C.	L	32.10±(21.88)^a	78.13±(22.85)^a	21.17±(24.64)^b	42.18±(18.44)^a	78.25±(17.76)^a	10.97±(19.46)^b
	BD	1.11±(0.03)^a	0.91±(0.02)^b	1.17±(0.05)^a	1.15±(0.03)^a	1.01±(0.02)^a	1.09±(0.02)^a
	RD	14.38±(2.41)^a	21.84±(2.01)^a	8.18±(2.30)^b	13.96±(2.02)^b	20.26±(1.87)^a	10.17±(1.85)^b
W C	L	5.15±(3.44)^b	10.36±(2.89)^a	7.55±(3.03)^b	3.73±(4.28)^b	10.31±(3.35)^a	7.91±(3.42)^a
	BD	1.25±(0.05)^a	0.81±(0.01)^b	1.28±(0.05)^a	1.22±(0.05)^a	0.79±(0.01)^a	1.20±(0.05)^a
	RD	10.58±(3.05)a	15.62±(2,60)^a	7.10±(2.93)^b	18.33±(2.47)^a	24.54±(2.28)^a	12.60±(2.26)^b

3.5.3 Trenching

Total R_S rates ranged from 0.98 to 7.30 µmol m^{-2} s^{-1} in control plots and 0.10 to 5.84 µmol m^{-2} s^{-1} in trenched plots, with the mean of 4.98 µmol m^{-2} s^{-1} (control plots) and 4.26 µmol m^{-2} s^{-1} in the trenched plots. Overall, trenched plots emitted a mean of 3.44 (±0.42) and 4.26 (±0.48) CO_2 µmol m^{-2} s^{-1} during winter and spring. Soil CO_2 efflux were significantly different between seasons and were higher in control compared to trenched plots during summer and autumn seasons ($F_{[5, 189]} = 6.84$, $p = 0.000$, $n = 13$) (Figure 3.3; Table 3.4).

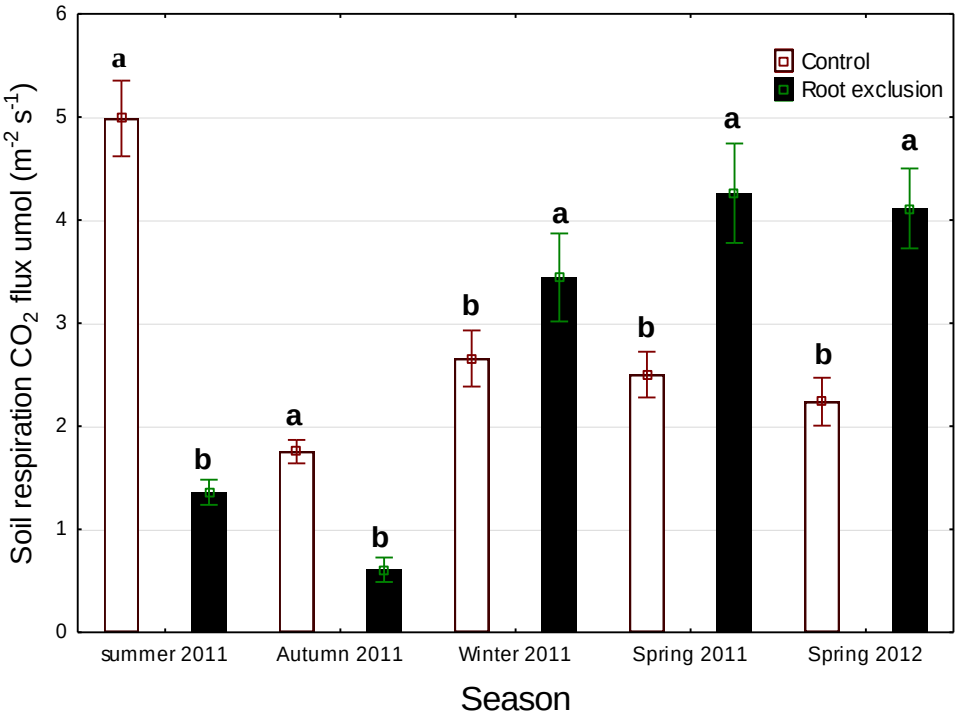

Figure 3.3: Average soil respiration from control and root exclusion plots from three invaded riparian sites. Data are from summer to spring 2011 with an exceptional single season measured one year later after trenches installation (spring 2012). Measurements were taken within the dry banks of the invaded sites. Plain bars represented control CO_2 efflux (intact plots) and black columns stand for CO_2 efflux from trenching plots (Root exclusion). Bars represent means and box whisker standard errors at 95 % confidence intervals for both intact and trenche plots. Significance levels LSD: $p < 0.05$ are indicated by different letters for one-way analyse of variances.

However, the high CO_2 efflux observed in control plots shifted in winter and spring and was highest in root exclusion plots. It remained high during the spring of 2012, one year after the last measurement, in spring 2011. Increase CO_2 efflux showed considerable seasonal variations between winter and spring 2011. Soil respiration dramatically dropped from 4.98 µmol m^{-2} s^{-1} in the control to 2.66 µmol m^{-2} s^{-1} and in the trenched plots after root was cut off with mean value of 1.36 µmol m^{-2} s^{-1} recorded in summer and 3.44 µmol m^{-2} s^{-1} in winter 2011. Soil respiration was highest in control during summer and deceased to 46 % in winter. We observed a decrease in R_S during autumn for control plots from 46 % to 34.2 %. Soil respiration remained lower during two seasons with decreased R_S rates of up to 82 % in autumn 2011 (figure 3.3), while it increases to 60 % three seasons late after roots were removed during winter.

Table 0.4: Analysis of variance (ANOVA) for invaded riparian zones versus treatment and seasons and surface CO2 efflux µmol m^{-2} s^{-1} (0-5cm depth) from summer 2011 to spring 2011. With an extract special season: spring 2012. DF: Degrees of freedom, *F*: *S*tatistics, *P*: Probability *F* value at P < 0.05.

Trenching	DF	F	*P*-values	Significance
Season	3	15.42	0.000	*
Treatment	1	72.80	0.013	*
Season X Treatment	3	43.52	0.000	*
Control				
Season	3	23.41	0.000	*
Treatment	1	77.89	0.012	*
Season X Treatment	3	37.93	0.000	*

: indicates significant difference at P < 0.05.

3.6 DISCUSSION

In addition to *in situ* measurements of R_S that was carried out over seven seasons, we also carried out *ex situ* measurements of R_S where the effect of roots was excluded. We did the latter by incubating soils from each of the sites, inclusive of the different landscape positions and the different invasion statuses at a constant temperature and moisture level. We also sampled soils from the same sites in the Western Cape where the *in situ* measurement has been carried out, but also from a series of secondary sites. The objective was to determine the role that microbial respiration played in overall R_S, and to ascertain whether general trends emerged.

Our results show that there were, on average little significant differences emerged between PR_S values obtained from soils sampled from different invasion status. Although we found differences in sampling dates i.e. a fast rise in PR_S rate, which later declines), this is likely the results of different types of carbon (labile vs. recalcitrant; Bechtold and Naiman, 2006; Gu et al., 2004). Booi (2010) found differences in PR_S when soils from succulent Karoo, sampled on and off heuweltjies (similar to 'mima-like' mounds) were incubated at constant temperature and moisture levels. Heuweltjies have significantly different soils and vegetation. The difference that emerged was attributed to inherently different soil microbial biomass, and which was expressed in different rates of respiration. Similarly, results were found by Jenkins and Mark (2010) but were different to that found by Bowden et al. (1997) who showed that CO_2 efflux increased exponentially with increasing temperature in forest floor material, with fluxes reduced at the

lowest and highest soil moisture contents suggesting that CO_2 efflux was controlled primarily by soil biological activity. Our data agree with study by Jenkins and Mark (2010) who found prominent differences in rates of PR_S among soils collected from a range vegetation types in subalpines ecosystems (Australia) that were geologically identical and varied only slightly in climate and topography. Wagner et al. (1996) concluded that investigating microcosm and soil suspension studies were designed to uncouple the *in situ* system and reveal the anaerobic capacities of theoretical micro-sites. Therefore, one can make the assumption that at a broad level, differences in microbial biomass did not drive differences in PR_S of sites with different invasion status observed in the field.

In addition, in the field, most of the differences emerge in summer, with hardly any differences between the different sites in the other seasons. This suggests that another factor, other than microbial populations may be at play. From work by Miller et al. (1983), it is clear that fynbos species are predominantly photosynthetically active during early summer and that stomatal conductance, and hence carbon capture declines later as the dry season progresses. Activity is much higher than in the winter and autumn. For *Acacia mearnsii*, Dye et al. (2001) found that evapotranspiration and sapflow is highest in summer, but again, this declines later when the seasonal drought progresses. *Acacia* spp. was found to be more profligate water users, and this may be at the core of its ability to outcompete native species in the fynbos. It is likely that the phenology and its associated physiological dynamics play a role in the observed responses we measured in the field. Högberg and Read (2006) suggested that photosynthate captured by trees are rapidly converted to carbon respired by the roots, and that this may happen on a time span of hours. Thus, while plant ecophysiology fell outside of the scope of this thesis, it likely played a more significant role in driving R_S in summer than microbial respiration.

On the other hand, we measured higher root mass (measured as once of samplings) in invaded riparian dry banks compared to other landscapes, and to the natural and the cleared sites. While on its own this does not suggest a causal link between R_S and roots, combined with our contention that plant physiology play a significant role in overall R_S rates, higher root density in *Acacia* invaded sites (see also Morris et al., 2011) may also contribute to the elevated respiration rates in invaded sites.

We attempted to isolate the role of roots in invaded sites by trenching areas within *Acacia*-invaded sites which lend themselves to digging trenches. After leaving trenched areas to equilibrate, we measured a 40 % decline in R_S in these plots compared to un-trenched controls.

Jauhiainen et al. (2012), working in *Acacia* plantations found that there was a decline in R_S rate, which allowed them to work out a contribution of plant roots to overall R_S, which amounted to between 56 and 21 % contribution of root respiration, depending on treatment. The contribution of autotrophic respiration to CO_2 efflux was found to be 21 % on average along transects in mature *Acacia* tree stands. Significantly higher heterotrophic respiration occurred very close to *Acacia* trees, but was negligible within treatment (distances between the measurement transects), indicating that measured CO_2 effluxes well away from trees were free of any contribution from autotrophic and represented heterotrophic respiration only (Jauhiainen et al., 2012).

The decline we found also suggested a large role for autotrophic respiration, however, when the plots were monitored over time, we found that the initial difference between the trenched and non-trenched plots disappear, and indeed subsequently, the trenched plots showed higher R_S rates. This result is puzzling, however, may be attributed to decomposition of organic matter and severed roots. We showed that soil moisture was higher inside the trenched areas when R_S rates were higher during later sampling times, which suggest this may be faster decomposition rates due to more moist conditions, and this may be a relic of the method we used (blast sheeting, which may have retained moisture), rather than a true reflection of root respiration. It is unlikely that fine roots grew into the trenched plots from outside and we did not notice any fine roots below 40 cm soil depth when the trenches were dug.

Some smaller differences emerged when comparing soils from different landscape positions. On average, PR_S values from dry banks were significantly higher than that of soils from native sites. This is consistent with the results of Goldstein et al. (2000) and Curiel-Yuste et al, (2007), who found that soils from different positions in the landscape showed significant differences in PR_S. Thus one can deduce that soil microbial biomass did play a role in the differences in PR_S of soil from different landscape positions, as found in the field (Chapter 3). While microbial biomass was not measured at these sites, Slabbert (2012) measured fungal and bacterial diversity and found that especially bacterial population structure was significantly different in wet banks compared to the higher elevation sites (dry bank and terrestrial are). From our results it appears that the overall activity, measured as PR_S of the bacterial populations may also be different. In addition, root mass was also highest in dry banks, which suggests more contribution of the plants itself to overall R_S rates measured.

3.7 CONCLUSION

It was found that roots are the likely most significant contributor to overall R_S compared to microbial respiration. The incubation of soils from different landscape positions and invasion statuses is a novel way to separate our autotrophic and heterotrophic respiration, and showed that the microbial biomass was likely similar in different types of sites (by invasion status), though landscape position did show differences which may be linked to microbial biomass. Indeed invaded dry banks had both the highest root mass, and also the highest R_S rates *in situ*, which suggest more likely that the roots are more important than microbes in determining overall R_S rates. We were unable to confirm this through trenching, which proved to be problematic, and some more research is needed to confirm these trends.

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CHAPTER 4

GENERAL DISCUSSION: CARBON CYCLING IN ACACIA-INVADED OF THE SOUTH-WESTERN CAPE FYNBOS ECOSYSTEMS

4.1 INTRODUCTION

Limited information is available on carbon cycling in soils of different Mediterranean ecosystems (Pinzari et al., 1999; Reichstein et al., 2002; Jarvis et al., 2007; Bond-Lamberty and Thomson, 2010) however; even fewer studies have focus on riparian and wetland CO_2 efflux. As far as could be ascertained, no studies have focussed on riparian areas in the fynbos biome in South Africa. Riparian soils store about one quarter of total carbon stored in soils in the world and so they are very important pools of carbon which may be released to the atmosphere if the ecosystems are disrupted (Andrews et al., 1999; Xu and Qi, 2001; Davidson et al., 2000). Riparian zones in the fynbos biome are heavily degraded due to multiple anthropogenic and natural disturbances; however, the most significant threat is invasive alien plant species, notably *Acacia mearnsii* and other *Acacia* species (Le Maitre et al., 1996; Funk and Vitousek, 2007; Le Maitre et al., 2007; Le Maitre et al., 2011). A major clearing effort is underway (the Working for Water Program) as it has been shown that invasive acacias in riparian zones are profligate water users, hence are affecting ecosystem services, especially in terms of water supply to ecosystems and people (Dye et al., 2001; Dye and Jarmain, 2004). A major assumption underlies the Working for Water (WfW) program, in that self-repair is thought to take place in riparian zones after clearing of the invasive *Acacia* spp., even though some studies have shown that this is not necessarily the case.

4.2 THE IMPACT OF INVASION ON SOIL RESPIRATION

Our study showed that invasion and establishment of *Acacia mearnsii* and associated *Acacia* spp. in fynbos riparian zones fundamentally alter soil C cycling. It is apparent that dry banks house the highest density of *Acacia* species and invaded dry banks were also where the highest rates of R_S was documented. On average CO_2 emission rates were twice and more what it was from soils under native plant communities. However, the most prominent difference appeared in summer, when soils were relatively dry, but when temperatures were high. While we did not investigate this, photosynthesis rates in terrestrial fynbos peaks in summer, and declines later in summer as summer drought takes hold. This suggests that plant physiology rather than inherent

soil properties may play a major role in observed increases in R_S during summer (Ehleringer et al., 1997; Bhupinderpal et al., 2003). Indeed, when we eliminated the potential impacts of roots by incubation soils (minus roots) in microcosm and then measuring soil CO_2 efflux, little differences were evident between sites with different invasion status (reference versus invaded). While our trenching experiment did not show consistent trends, enough evidence exist that root respiration are driving overall soil respiration in summer. Our results are consistent with those of Juahainen et al. (2012), who found higher contribution of roots to overall soil respiration closer to *A. mearnsii* trees growing in a plantation rather than farther away, where microbial respiration became more important. Since the *Acacia mearnsii* trees invading fynbos riparian zones often grown in very dense stands, it is likely that roots density is also much higher than native riparian zones, and indeed, we found higher root mass. Indeed, it is suggested that invasive acacias outcompete native spices, partially through faster root growth and density (Funk and Vitousek, 2007; Morris et al., 2011).

4.3 THE EFFECT OF CLEARING ON SOIL RESPIRATION

We found that R_S rates decline significantly when invasive Acacia individuals are removed from riparian zones, more particularly dry banks. Root mass was lower in cleared riparian dry banks compared to invaded dry banks and natural areas. These trends suggest that ecosystem function, as it related to C cycling recover after removal of the invasive individuals, and that the restoration trajectory is towards the pre-invasion condition. In a parallel study at the same sites, Naudé (2012) also found that other soil chemical and biochemical properties, notably acid soil phosphate monoesterase activities return to the natural condition, which is also seen is a key component of soil ecosystem functioning in fynbos riparian ecotones, especially as P is in short supply in fynbos soils, and also in riparian soils. Overall, then, this demonstrates the positive influence of clearing on ecosystem functioning. However, caution should be exercised as this cannot necessarily be extrapolated to other aspects of ecosystem function.

4.4 IMPORTANCE OF THIS STUDY

The general objective of this study was to investigate R_S in riparian zones of the south-western Cape with invasion by IAPs and compare that to a reference condition, and cleared riparian ecotones in order to understand the key role of biotic and abiotic factors in the process of carbon cycling in fynbos riparian zone. We show that R_S is enhanced significantly by *Acacia* invasion; however, than clearing lead to declines, and cleared riparian ecotones appear to be in

a trajectory back to the pre-invasion state. This should provide additional impetus to WfW that clearing indeed restore ecosystem function, at least as far as C cycling is concerned. Other aspects or ecosystem functioning was not investigated, hence cannot be commented on further. However, another important consideration is the relative contribution of *Acacia* trees to C sequestration, and the C balance of invaded areas, which covers as much as 100 000 km^2, which is over 8 % of the country's total area (van Wilgen et al., 2001; de Wit et al., 2001).

4.5 FURTHER RESEARCH

An important next step is to investigate the C balance of invaded riparian ecotones, and indeed also terrestrial areas that has been invaded by *Acacia* species. It has been suggested that a 'positive' result of invasion of South African ecosystems with woody alien invasive plants is that these plants grow fast, and hence sequester C, which may counteract increasing global CO_2 emissions in a small way. We showed that CO_2 emissions increase tremendously in invaded riparian ecotones, however, the overall balance of C in these areas remain unclear. If the increase in R_S seen here is universal, then this provide more motivation for clearing riparian ecotones and upland areas, however, this remains to be investigated.

Furthermore, some more in depth investigation of drivers of soil respiration, both in riparian and upland environments is needed, using longer-term trenching, microcosm studies and other techniques are need to get to the bottom of the main drivers of R_S.

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Appendix 1: CO_2 flux arranged by landscape positions versus soil temperature and GSWC

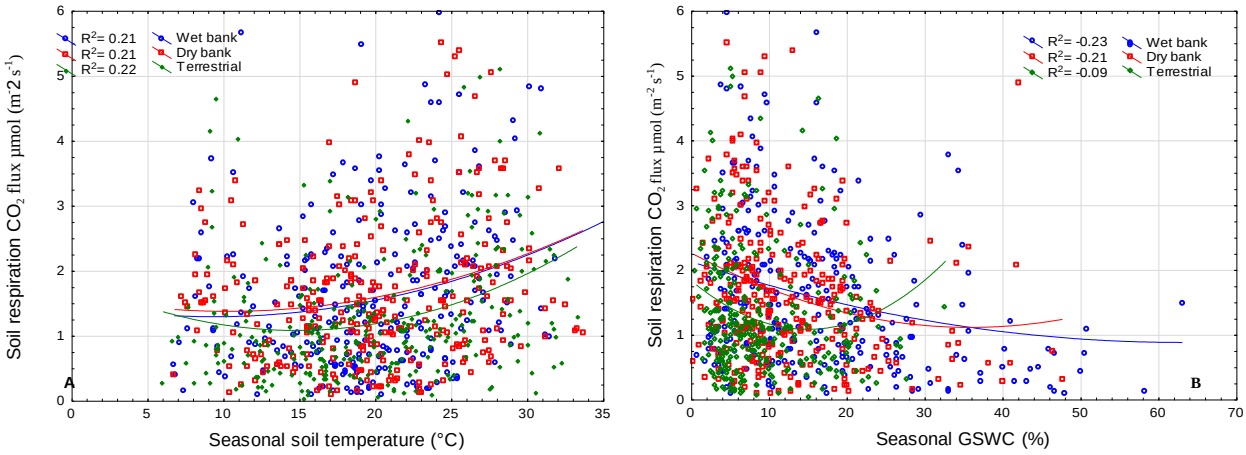

Figure A1.1: Seasonal relationship between soil respiration and soil temperature by landscape positions within wet bank, dry bank, and terrestrial upland adjacent fynbos (A) and soil respiration against gravimetric soil water content (GSWC %) across micro-sites (B) during seven seasons from autumn 2010 to spring 2011.

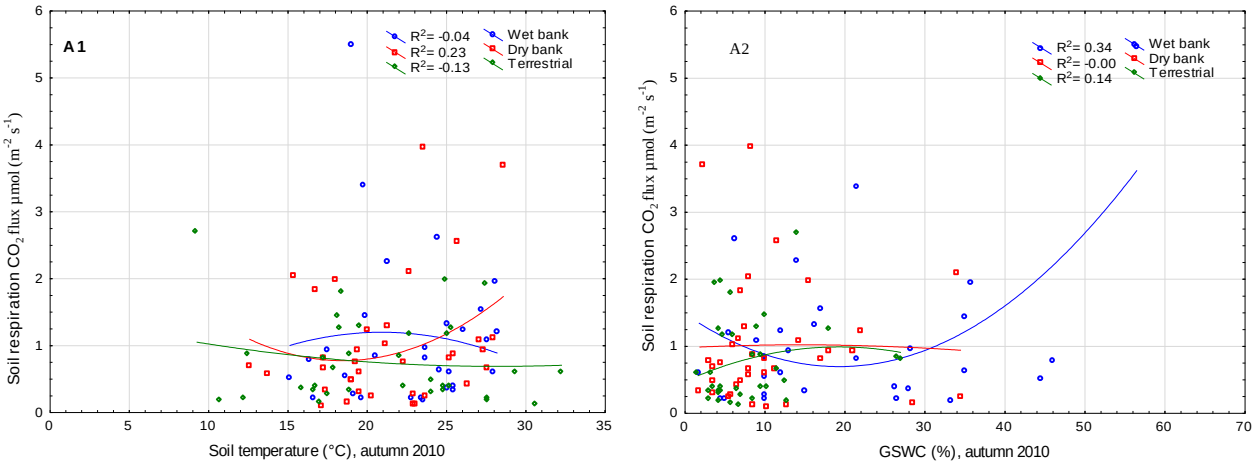

Figure A1.2: Mean soil respiration (µmol m^{-2} s^{-1}) plotted against mean soil temperature and gravimetric soil water content (GSWC) gathered by season and across landscape positions from autumn 2010 to spring 2011. From left (R_S vs. soil temperature) and right panel is the relationship between RS plotted against GSWC (right) (A1, B1, C1, D1, E1, F1, and G1), for autumn 2010 up to spring 2011 (A2-G2).

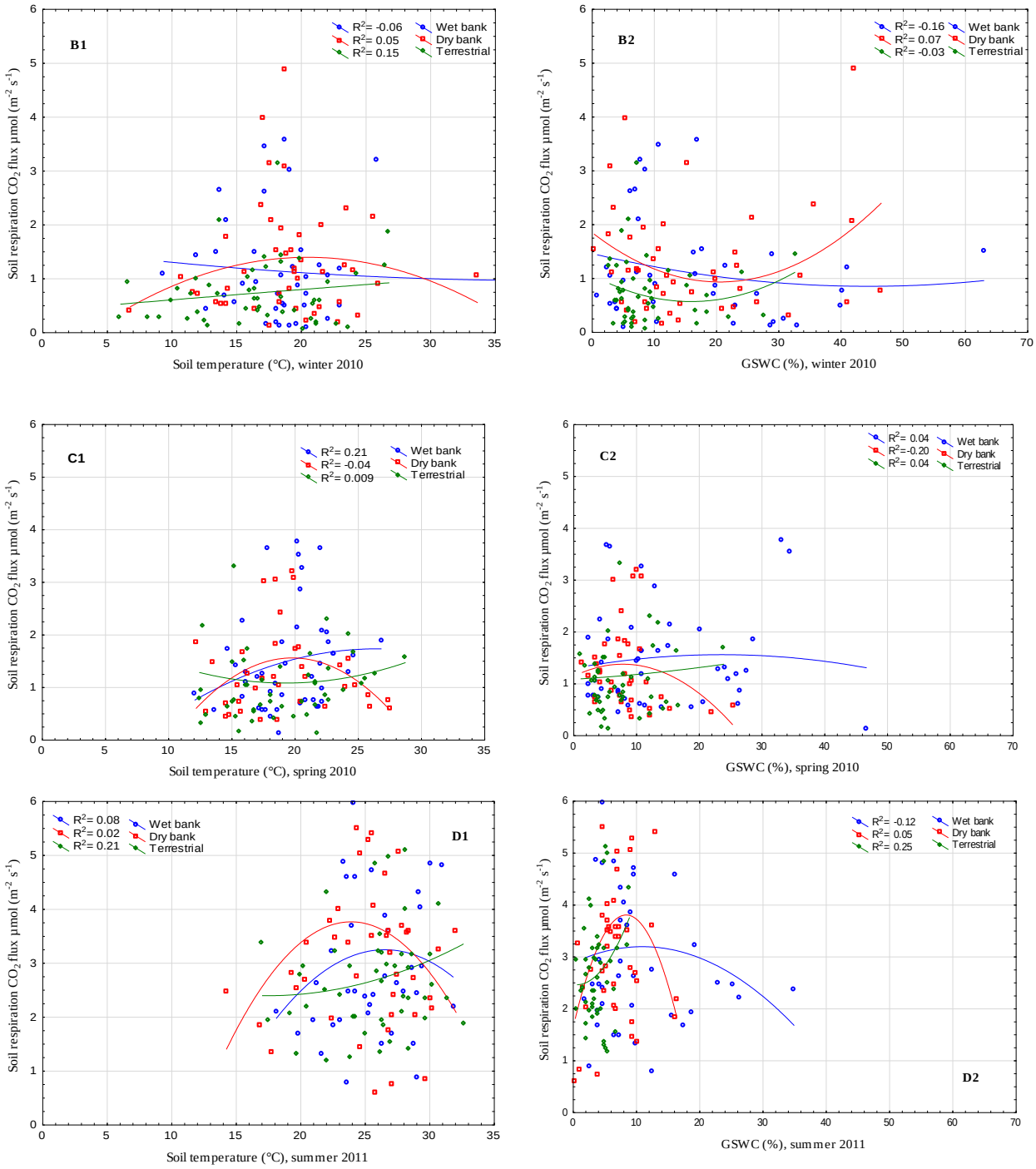

Figure A1.2 (continued). Mean R_S (µmol m^{-2} s^{-1}) plotted against mean soil temperature and gravimetric soil water content (GSWC) gathered by season and across landscape positions. R_S vs. soil temperature (B1, C1, D1), and R_S plotted against GSWC (B2, C2, and D2).

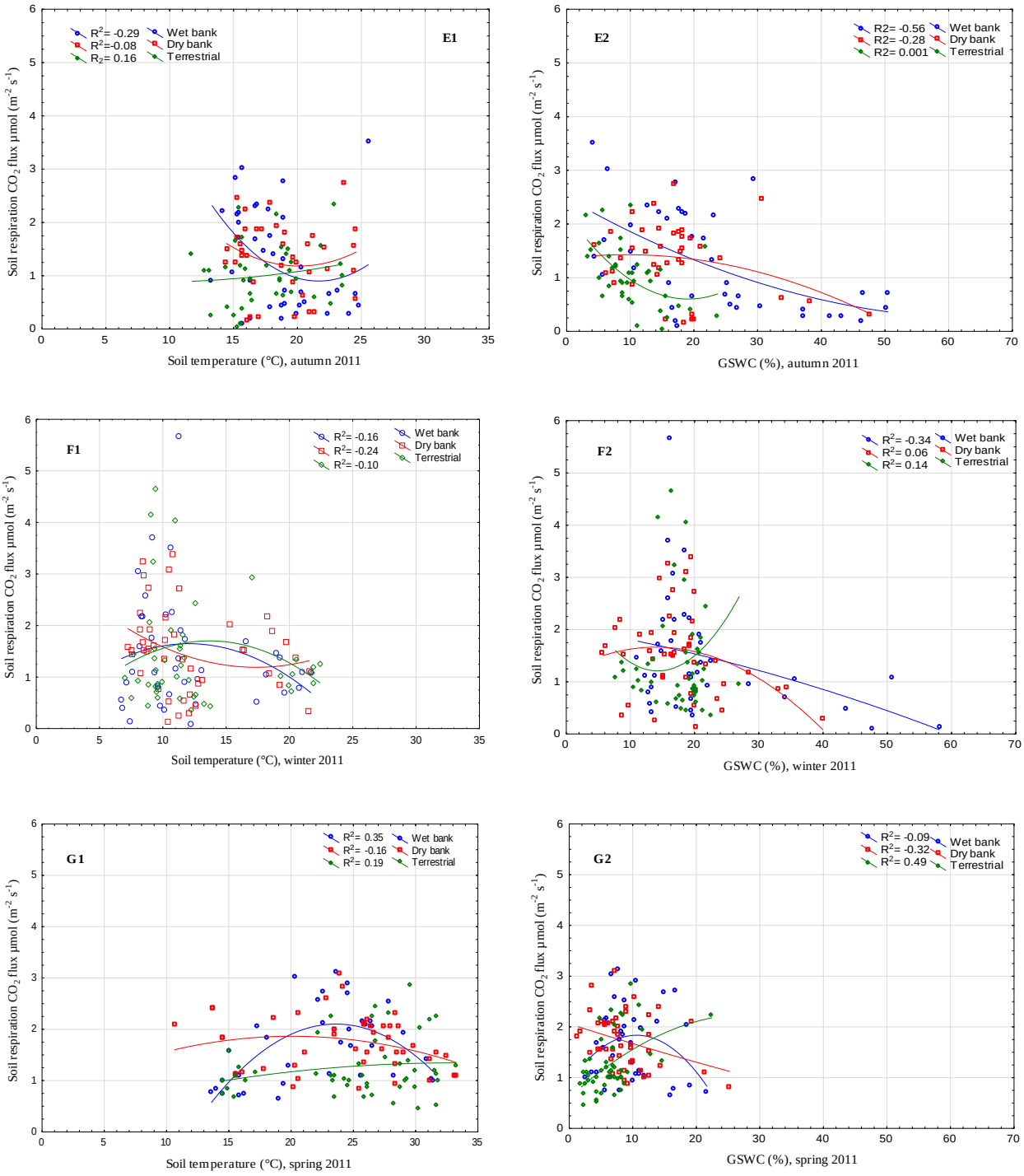

Figure A1.2 (continued). Mean R_S (µmol m^{-2} s^{-1}) plotted against mean soil temperature (E1, F1, and G1) and gravimetric soil water content (GSWC: E2, F2, and G2).

Appendix 2: Mean soil respiration, soil temperature and GSWC by season

Table A2.1 Seasonal soil respiration rates µmol (m^{-2} s^{-1}), soil temperature (°C), GSWC (%), soil bulk density (BD) and root mass (RD). values are means and standard errors only and are arranged by invasion status and landscape positions.

R_S CO_2 flux µmol ($m^{-2}s^{-1}$)			Invasion status			Landscape position		
			Natural	Invaded	Cleared	Wet bank	Dry bank	Terrestrial
Season	Source	Mean ±S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.
Autumn 2010	RS	1.06 ± 0.13	0.80 ± 0.22	1.58 ± 0.26	0.81 ± 0.21	1.26 ± 0.19	1.09 ± 0.18	0.84 ± 0.18
	TS	21.31 ± 1.00	22.94 ± 1.68	19.99 ± 1.87	21.00 ± 1.66	21.85 ± 1.12	21.03 ± 1.10	21.05 ± 1.12
	GSWC	13.54 ± 1.18	14.03 ± 1.98	16.15 ± 2.25	10.46 ± 1.86	21.00 ± 1.72	10.97 ± 1.61	8.66 ± 1.67
Winter 2010	RS	1.05 ± 0.12	0.75 ± 0.22	1.41 ± 0.21	1.00 ± 0.18	1.13 ± 0.17	1.30 ± 0.16	0.72 ± 0.15
	TS	17.88 ± 0.92	16.84 ± 1.68	18.27 ± 1.67	18.54 ± 1.44	18.16 ± 1.04	18.79 ± 1.00	16.70 ± 0.99
	GSWC	13.83 ± 1.06	15.03 ± 1.98	9.68 ± 1.87	16.77 ± 1.63	15.78 ± 1.57	16.07 ± 1.44	9.64 ± 1.41
Spring 2010	RS	1.26 ± 0.12	1.03 ± 0.22	1.76 ± 0.18	1.00 ± 0.21	1.40 ± 0.16	1.23 ± 0.17	1.16 ± 0.15
	TS	19.28 ± 0.92	19.72 ± 1.68	20.19 ± 1.45	17.94 ± 1.67	20.13 ± 1.02	18.88 ± 1.04	18.84 ± 0.99
	GSWC	9.75 ± 1.07	7.55 ± 1.98	10.14 ± 1.67	11.54 ± 1.90	13.28 ± 1.53	8.71 ± 1.56	7.24 ± 1.42
Summer 2011	RS	2.94 ± 0.12	2.55 ± 0.21	4.18 ± 0.18	2.09 ± 0.21	2.91 ± 0.16	3.22 ± 0.15	2.69 ± 0.15
	TS	25.44 ± 0.92	23.84 ± 1.67	26.47 ± 1.44	26.01 ± 1.66	25.45 ± 1.02	25.22 ± 1.00	25.66 ± 0.99
	GSWC	7.04 ± 1.05	9.92 ± 1.95	6.36 ± 1.65	4.84 ± 1.87	10.66 ± 1.51	6.62 ± 1.44	3.85 ± 1.42
Autumn 2011	RS	1.19 ± 0.13	1.11 ± 0.26	1.53 ± 0.18	0.93 ± 0.21	1.31 ± 0.17	1.26 ± 0.17	0.99 ± 0.17
	TS	18.22 ± 1.00	16.04 ± 2.05	17.00 ± 1.44	21.62 ± 1.66	18.45 ± 1.09	18.63 ± 1.09	17.59 ±1.10
	GSWC	16.28 ± 1.13	13.01 ± 2.30	14.92 ± 1.65	20.92 ± 1.87	21.37 ± 1.58	16.59 ± 1.57	10.88 ± 1.57
Winter 2011	RS	1.44 ± 0.12	0.93 ± 0.21	1.75 ± 0.18	1.66 ± 0.21	1.36 ± 0.17	1.49 ± 0.15	1.48 ± 0.15
	TS	12.18 ± 0.92	15.18 ± 1.68	12.03 ± 1.44	9.32 ± 1.66	12.01 ± 1.03	12.01 ± 1.00	12.50 ± 0.99
	GSWC	19.60 ± 1.06	24.52 ± 1.97	17.39 ± 1.65	16.88 ± 1.87	23.11 ± 1.55	18.06 ± 1.44	17.63 ± 1.42
Spring 2011	RS	1.53 ± 0.12	1.31 ± 0.21	1.74 ± 0.18	1.54 ± 0.21	1.59 ± 0.17	1.70 ± 0.15	1.29 ± 0.15
	TS	23.92 ± 0.92	19.98 ± 1.67	25.77 ± 1.44	26.02 ± 1.66	22.74 ± 1.03	23.96 ± 1.00	25.07 ± 0.99
	GSWC	8.37 ± 1.06	9.58 ± 1.96	6.52 ± 1.66	9.00 ± 1.86	9.46 ± 1.56	8.91 ± 1.43	6.74 ± 1.42
Autumn 2011	BD (g soil cm^{-3})	1.07 ± 0.02	1.11 ± 0.04	1.12 ± 0.03	1.08 ± 0.03	1.17 ± 0.03	1.05 ± 0.02	1.09 ± 0.02
Spring 2011	RD (Kgm^3)	18.49 ± 1.65	14.38 ± 2.41	21.83 ± 2.01	8.17 ± 2.28	13.96 ± 2.01	20.26 ± 1.87	10.17 ± 1.85